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Distribution of Liocarcinus depurator along the western Mediterranean coast

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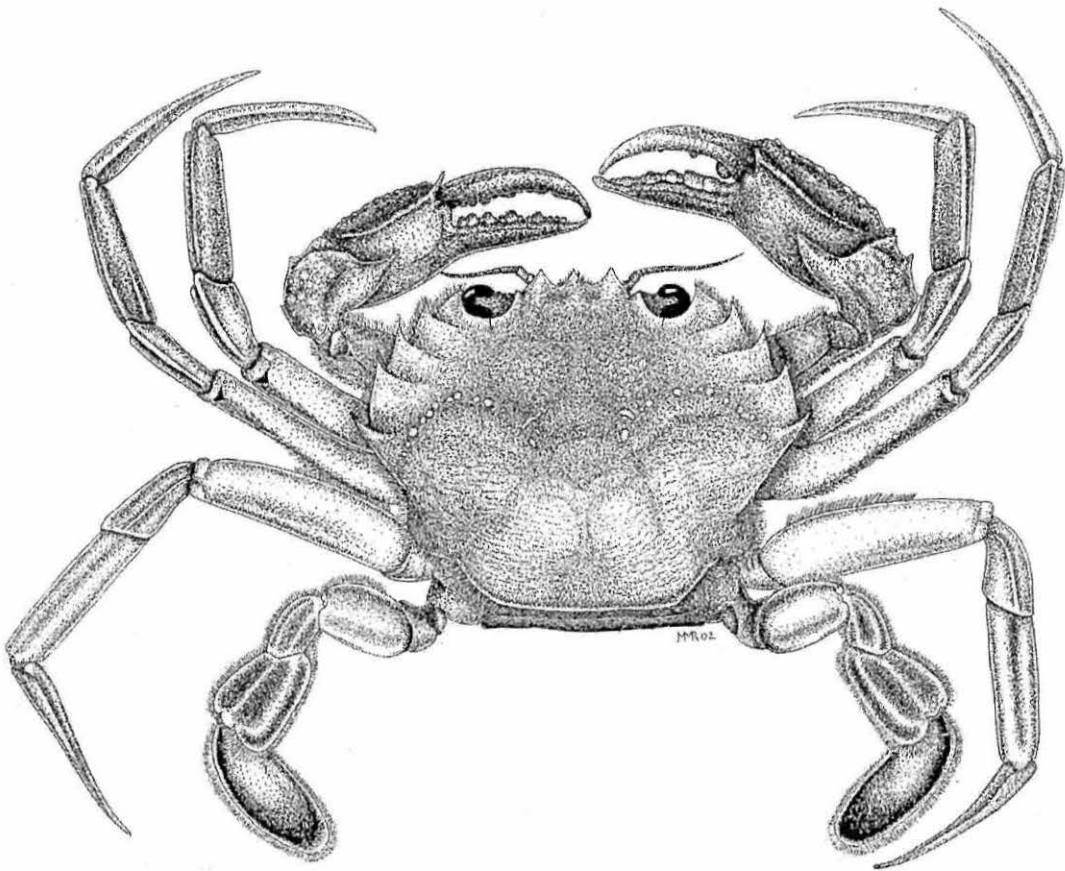
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DISTRIBUTION OF *LIOCARCINUS DEPURATOR* ALONG THE WESTERN MEDITERRANEAN COAST

By

Marta M. Rufino

A thesis submitted to the University of Wales, Bangor. School of Ocean Sciences for the degree of Doctor in Philosophy

This thesis is dedicated
to my mum, without whom
none would have been possible

Summary

The distribution of *L. depurator* has been analysed through classical statistics, linear models and geostatistics. Density was obtained from a ten-year time series of bottom, otter trawl surveys in eight areas along the Mediterranean coast of Spain. Two peaks of *L. depurator* occurrence were observed. The first (80% occurrence) between 51 and 150 m, and the other (66% occurrence) between 301 and 400 m. Below 500 m, crab occurrence was negligible (<8%) and densities fell sharply. The pattern shown by crab densities closely shadows that of occurrence, although a second abundance peak was barely evident, and was located at 201-300 m. From 200-400 m, crab abundance appeared fairly evenly distributed but showing lower densities than in shallower waters.

Analysis through linear modelling showed that *L. depurator* density decreased significantly with depth and year, but no effect of sample location was evident. The decrease of *L. depurator* density was most pronounced at shallower depths (depths < 150 m, declining at ~8±1 % per annum), than in deeper waters (depths > 150 m, declining at ~4±1 % per annum).

Geostatistical analysis of *L. depurator* densities showed that the crabs distributions exhibited varying degrees of spatial structure with patch sizes varying between 19 and 75 km among the sampled years. When average densities were low, crabs were most abundant in Ebro River Delta area and Western Alborán Sea, areas showing permanent high-density populations. The virtues and drawbacks of each approach are discussed.

On a smaller scale, off the Ebro Delta *L. depurator* distribution (numbers and biomass) was related to sediment characteristics using geostatistics. Smaller crabs were found preferentially in shallower water, whereas larger crabs, in deeper ones.

Given the presence of at least two distinctive aggregations (possible populations) of *L. depurator* on the Spanish coast, a series of morphometric studies were undertaken. A combination of traditional dimension analysis and geometric morphometry (whole shape analysis) was used to compare crab morphology. Differences in carapace shape were identified between genders and geographic location that largely appeared to involve the abdomen width.

Table of contents

List of Figures

List of Tables

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I. General introduction

I-1. THE DISTRIBUTION OF *LIOCARCINUS DEPURATOR*

Liocarcinus depurator is an eurythermal temperate species (Christiansen, 1982; Pérès & Picard, 1965) with a wide bathymetric range (continental shelf and upper slope) and habitat (Abelló & Valladares, 1988; Minervini *et al.*, 1982; Zariquiey-Álvarez, 1968).

This species was the dominant brachyuran by-catch in Mediterranean demersal fisheries down to depths of 200 m (Abelló *et al.*, 1988; Sardà & Palomera, 1981). In the Cantabrian Sea (Ribadeo to Fuenterrabia) and Galicia (western Atlantic Ocean) it was one of the most abundant species both on the continental shelf and in the 'Rías' (coastal embayments) (Ría de Arousa, Ría de Muros y Noia and Ría de Pontevedra), particularly in the mussel raft culture areas (i.e. most Galician Rías are exploited with mussel rafts)(Fariña *et al.*, 1997; García-Castrillo & Olaso, 1995; González-Gurriarán, 1986; González-Gurriarán *et al.*, 1993; González-Gurriarán & Olaso, 1987; Iglesias & González-Gurriarán, 1984; Olaso, 1990; Olaso & Rodriguez-Marín, 1995). In the Clyde Sea (Ireland) (Nickell & Moore, 1992), Scottish Lochs and Firths (Loch Gairloch and Loch Sween, Firth of Clyde) (Glass, 1985; Glass & Huntingford, 1988; Hall *et al.*, 1990a) *L. depurator* was noted among the eight most numerous brachyuran species. Sporadically, it is found intertidally at low tide in the Forth estuary (Scotland), tolerating salinities of 29-33 during the summer season (Mathieson & Berry, 1997), but it does not penetrate into the inner estuary.

Liocarcinus depurator is a common prey and predator of many marine commercial and non-commercial species (Hall *et al.*, 1990b; Olaso, 1990). However, predation pressure of *L. depurator* in a sandy Scottish loch (Hall *et al.*, 1990a), appeared to have little effect on subtidal species assemblages, but these crabs tend to prefer mud to sand.

I-2. GEOGRAPHIC DISTRIBUTION

L. depurator is distributed from the Eastern Atlantic coast, Northwest Africa (Marroco-Mauritania) to the Northeast Atlantic (West Norwegian coast, between Lofoten Islands and 65° N to the Sound and/or Belts; it is common till 68°N) and throughout the Mediterranean Sea. Figure I-1 shows the breadth of *L. depurator* distribution.

Figure I-1: Distribution of *L. depurator*. (+) represent occurrences around the UK, from Clark (1986); Numbers: 1: d'Udekem d'Acoz (1992), 2: Balkis *et al.* (2001), 3: Olaso (1990), 4: Fariña *et al.* (1997), 5: González-Perez (1995), 6: Monteiro *et al.* (2001), 7: Gaspar *et al.* (2003), 8: Sardà *et al.* (1982), 9: Rallo *et al.* (1993), 10: Gutie-rrez *et al.* (1989), 11: Abelló, et ,al. (2002), 12: Lewinsohn & Holthuis (1986), 13: Manning & Froglia (1982), 14: Spanò (1998), 15, Šimunovic (1997), 16: Ungaro *et al.* (1999a), 17: Mori & Zunino (1987), 18: Abelló *et al.* (1991), 19: Bedini *et al.* (2002), 20: Pipitone & Arcoleu (2003), 21: Minervini *et al.* (1982), 22: Christiansen (1982), 23: Schembri & Lanfranco (1984), 24: (North Sea) Basford *et al.* (1989) and Dyer *et al.* (1983), 25: Ates (1999). See Table I-3 for further details.
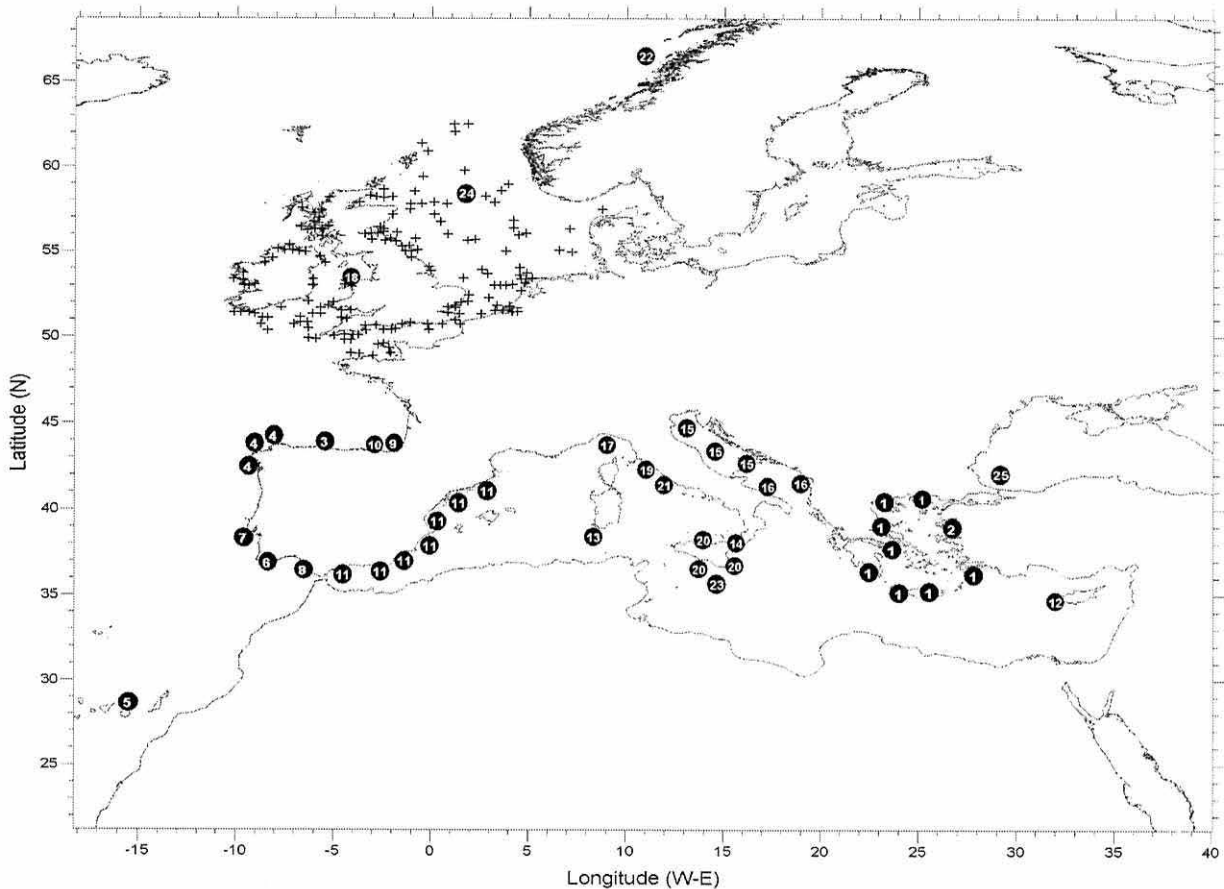
I- 2.1. Geographic variation in crab abundances

Figure I-2 shows *Liocarcinus depurator* abundances over its geographic range. Abundance measurements have been derived from using dredges, bottom and beam trawl, visual census and baited creels to name the most common. Díez *et al.* (1994) considered that the variability in abundances of *Liocarcinus depurator* in the Cap Bretón (Northwest France) were largely due to the capture method (bottom trawl or dredge) rather than the type of substratum. These authors found the crab occurred in 83% of bottom trawl samples (N=6) but only 41% of rock dredges (N=22). Density was likewise correlated with 16.8 crabs.30 min hauls and only 0.77 crabs.10 min dredge (Díez *et al.*, 1994) (Table I-3). Minervini *et al.* (1982) sampling the Tiber

estuary (Central Italy) caught no *L. depurator* using dredges, but the species was present in 50% of all bottom trawls.

With such disparity of results depending on the methods of capture it is very difficult to compare across studies. Furthermore, even within methods, the units reported vary. For example, for bottom trawl studies most present abundance in numbers of crabs per haul (either 30 min or 1 h haul) while recent works tend to report numbers of crabs per swept area. Thus, because different gear, trawling times, etc were used in each case, Figure I-2 can be thought of as approximate standardisation of *L. depurator* abundances throughout its distribution.

Despite differences in sampling methods, Figure I-2 provides an up-to-date picture of *L. depurator* abundances across its range. Along the Atlantic coast, densities were greater on the coast of France and Spain than in the North Sea (Figure I-2). In the Mediterranean, the central Adriatic clearly showed higher abundance of crabs than any other sampled area (Figure I-2).

The importance of *L. depurator* in the Galician Rías Baixas, contrasts sharply with its low density on the adjacent shelfs and abundances are much lower than on the Catalonia shelf (Fernández *et al.*, 1991). The Ría de Arousa (Galicia) high abundance of *L. depurator* is probably due to the presence of mussel culture and rich muddy sediments (Muiño, 1997). The maximum abundance and biomass values throughout Ría de Arousa, were 0.44 ind.m^{-2} and 8.80 wet g.m^{-2} caught at night during November. Crab densities, biomass and growth rates under mussel culture raft areas were significantly higher than in areas away from the rafts (Fernández *et al.*, 1991; González-Gurriarán *et al.*, 1995). Since many mussels fall from the rafts, along with general debris and detritus, the area under the rafts is probably ideal for a bivalves and worm-eating crab like *L. depurator* (Abelló & Cartes, 1987; Freire *et al.*, 1991a). The inner Ría de Arousa experiences salinity fluctuations due to the river run off, while the Outer Ría and the Central Channel have greater oceanic influence (Freire *et al.*, 1996). This may explain the lower biomass in the inner Ría (Table 3), despite the presence of the raft areas. The crab density in the Ría de Arousa was twice as high as in the Ría de Muros y Noia and twenty times higher than in the Ría Ferrol (Table I-3) (Freire *et al.*, 1993; González-Gurriarán, 1986; González-Gurriarán *et al.*, 1991; González-Gurriarán *et al.*, 1995; Iglesias & González-Gurriarán, 1984). Ría de Arousa has the most intensive mussel culture with 2000 rafts compared to the 70 in the Ría de Muros e Noia. The Ría de Ferrol is smaller and thinner than the others, with less habitat diversity, no mussel culture and industrial activity at its head (González-Gurriarán *et al.*, 1991).

Figure I-2: Standardised (to the same units) abundance of *Liocarcinus depurator*. The circles represent from 3 to 262 crabs, with the diameter of the circles being proportional to crab abundance. When values for several depths were provided, a global average was used. For Northern Longitudes above 50°N, densities are represented in crabs.1000 m^2, whereas southern values are in crabs.1 h haul. Whenever the units in the article were 30 min hauls, the densities were multiplied by 2. The areas covered by the surveys are covered in grey. Bathymetric lines are 200, 500 and 800 m. See table Table I-3 for further details on the samples. Note that as sampling methods, years and seasons diverge among the symbols, only relative comparisons are possible. Data from: Ligurian Sea: Mori & Zunino (1987); North Sea: Basford *et al.* (1989); Scottish Lochs: Hall *et al.* (1990a) and Glass & Huntingford (1988); Northern Adriatic Sea: Šimunovic (1997); Catalan Sea: Abelló *et al.* (1988); Galician coast: Fariña, et a. (1995); Cantabrian Sea: Olaso (1990); Ionian Sea: Politou *et al.* ; Cap Bretón: Rallo *et al.* (1993); Southern Adriatic: Ungaro *et al.* (1999a).
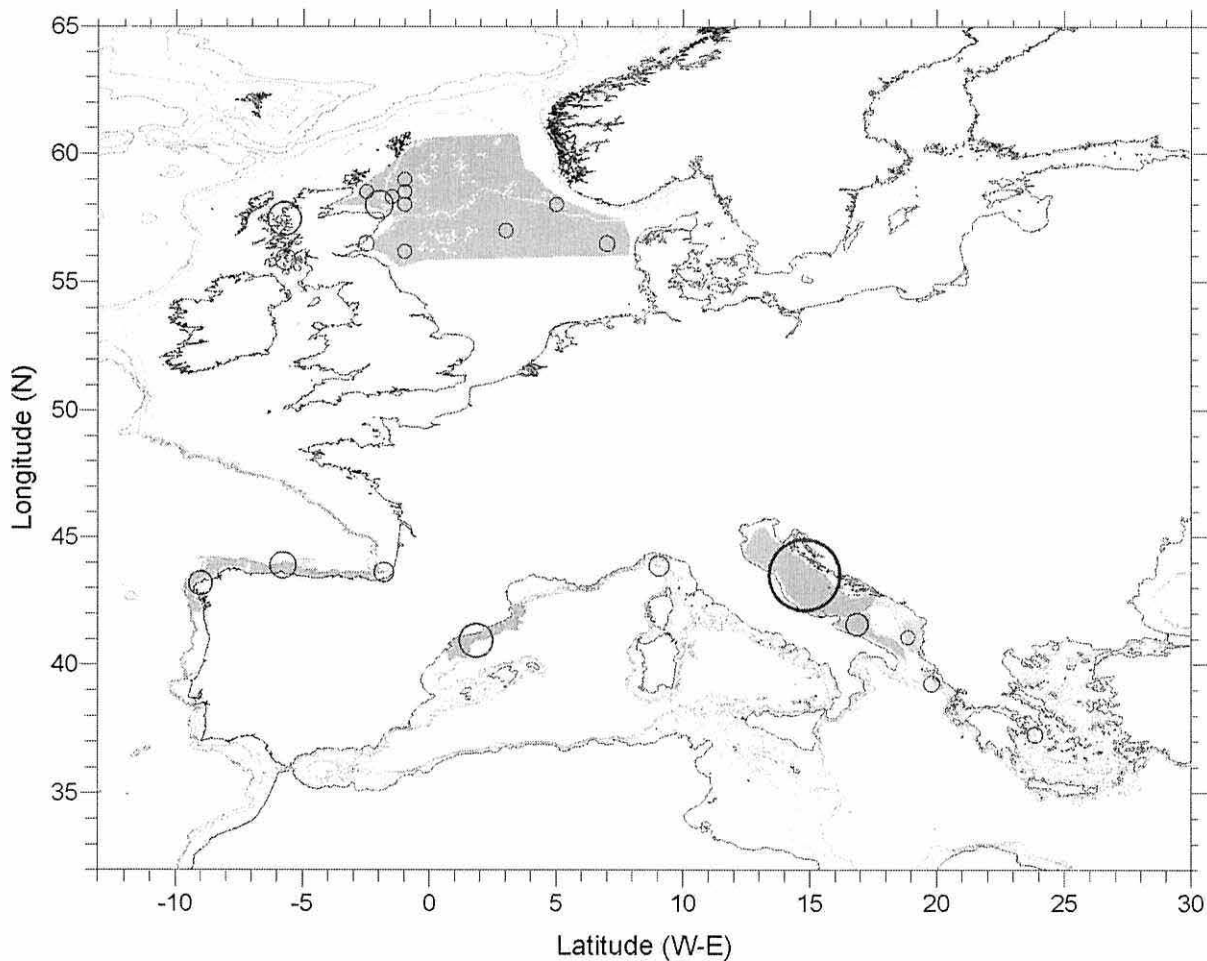
In low salinity Scottish estuaries, *L. depurator* densities were very low (Table I-3) with only 10 crabs caught in 10 years on the Forth estuary (Mathieson & Berry, 1997). Cartes *et al.* (1994) found that *L. depurator* densities were about twenty times greater in abundance in the shelf/slope transition zone than they were along the many submarine canyons off Barcelona (Cartes *et al.*, 1994). Seasonal changes in abundance were observed in the Cantabrian Sea (Olaso, 1990), Sardegna (Italy) (Mura, 1987), Galicia (Fariña *et al.*, 1997) and in the Catalan Sea (Abelló, 1986) (Figure I-4 and Figure I-5). In the Cantabrian Sea and North-Central Adriatic *L. depurator* abundances were greater in autumn-winter than during the spring (Fariña *et*

al., 1997; Šimunovic, 1997; Olaso, 1990), whereas along the Galician coast autumn densities were higher then the spring ones (Fariña *et al.*, 1997)(Table I-3). Off Cadiz (Atlantic south coast of Spain), there was a tendency towards greater catches of *L. depurator* during the summer months (Manjón-Cabeza & García Raso, 1998). In Ría de Arousa, winter crab abundances exceeded the summer ones (Fernández *et al.*, 1991). Peak *L. depurator* abundance in Loch Sween (Scotland) occurred at peak water temperatures from September to November (Glass, 1985). In the Adriatic Sea, crab density was three times higher on average in the Autumn/Winter surveys than in the Spring surveys (Šimunovic, 1997) (Table I-3). Thus it is difficult to generalise any seasonal behaviour of *L. depurator*, although seasonal differences were always present in all studies.

I-3. BATHYMETRIC DISTRIBUTION

Figure I-3 shows the depth distribution of *L. depurator* densities in the Atlantic and Mediterranean Sea. *L. depurator* maximum abundances were always shallower than 100 m in the Mediterranean and deeper than 100 m in the Atlantic (Figure I-3). In the Mediterranean, where surface waters are warmer then on the Atlantic coast, it might have been expected that the borearctic *L. depurator* would have been found at greater depths in the Mediterranean where the waters are cooler. Since such is not the case the depth distribution difference of *L. depurator* from the Atlantic to the Mediterranean must be driven by differences in habitat distribution, competing species or differences in prey distribution between the two areas.

Around the British Isles Clark (further references in Clark, 1986) notes *L. depurator* occurred from the lower shore to 280 m depth. Ingle (1980) considered that maximum densities in that area were located around 220 m depth. Lagardère (1973) observed a peak of *L. depurator* abundance around 150 m depth in the Gulf of Gascogne (Northwest France), although densities were low.

Along the Galician coast, the highest abundances were found deeper than 125 m (Figure I-3, Figure I-5 and Table I-3) (Fariña *et al.*, 1997; Fariña & Pereiro, 1995; González-Gurriarán & Olaso, 1987). Fariña *et al.* (1997) showed increasing crab densities from 1980 to 1987. Abundances were generally higher in the North than in the South (Fariña & Pereiro, 1995; González-Gurriarán *et al.*, 1993)

Figure I-3: *Liocarcinus depurator* maximum densities (black bar), in relation to the survey depths (grey bars). Data from Cap Bretón: Rallo *et al.* (1993); Cantabrian Sea: Olaso (1990); Galicia: Fariña *et al.* (1997); Catalan Sea: Abelló *et al.* (1988); Ligurian Sea: Mori & Zunino (1987); Adriatic: Šimunovic (1997); South Adriatic: Ungaro *et al.* (1999a).
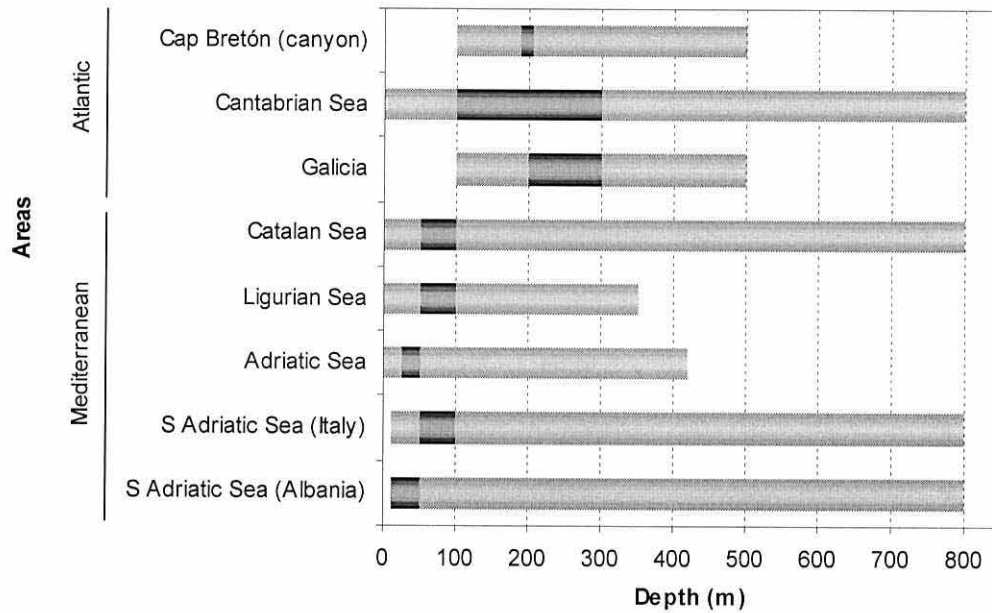
Figure I-4: Bathymetric seasonal density changes of *Liocarcinus depurator*.h^{-1} haul in the Galician coast (Northwest Spain)(Fariña & Pereiro, 1995), Cantabrian Sea (North Spain)(Olaso, 1990) and Adriatic Sea (North and Central Adriatic) (Šimunovic, 1997). Black dashed line with circles shows results from autumn/winter surveys whereas continuous grey line with triangles shows spring surveys. Note differences in graphs scales. The values from the Cantabrian Sea and Galicia were from 30 minute tows, thus multiplied by two. See Table I-3 for further details of the data.
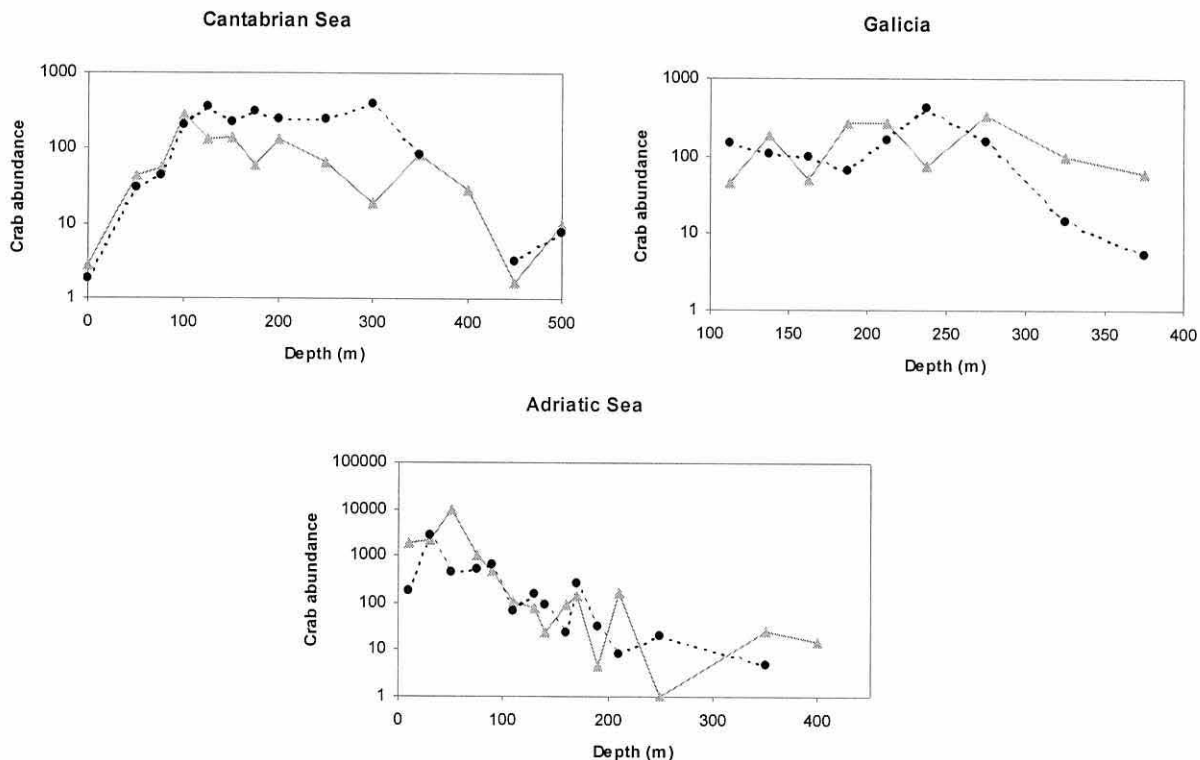
Figure I-5: Variation of the average $\log_{10}$ abundance of *Liocarcinus depurator* per 1 hour bottom trawl, with depth. Data from: Cantabrian Sea: Olaso (1990); Galician coast (extracted from the graph): Fariña *et al.* (1995); Catalan Sea: Abelló *et al.* (1988); Ligurian Sea: Mori & Zunino (1987); South Adriatic Sea: Ungaro *et al.* (1999a); Adriatic Sea (North and Central): Šimunovic (1997). The densities in the Cantabrian Sea and Galician coast were doubled, because the duration of the hauls was 30 min. See Table I-3 for further details of the data.
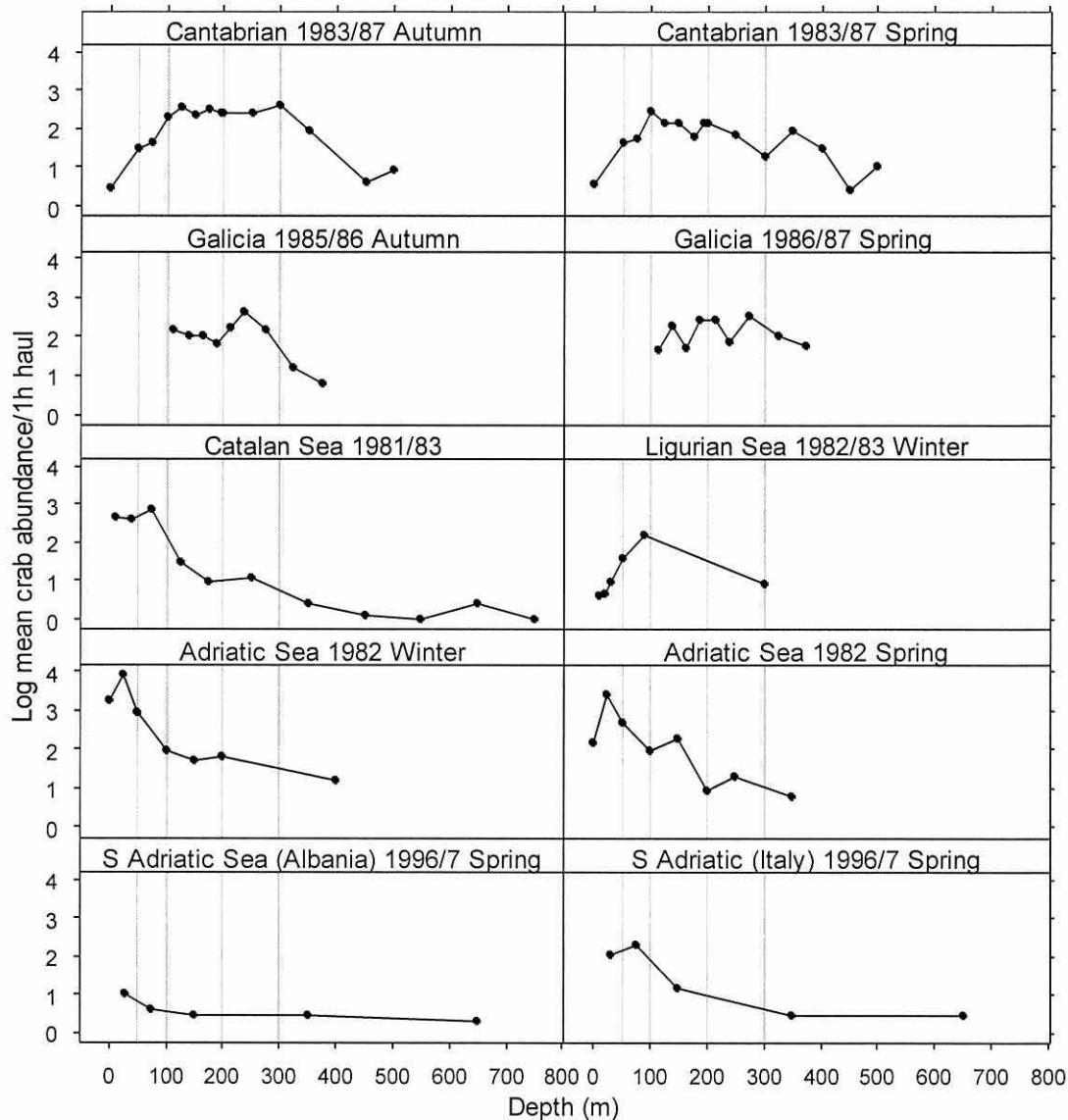
Bathymetric variation of *L. depurator* abundance, changed seasonally. During spring peak abundances were found at shallower depths than during autumn in the Cantabrian Sea (Olaso, 1990) (Figure I-4 and Figure I-5). In Galicia, during autumn high crab abundances were between 225-250 m depth, while during spring two peaks were observed, one at 175-200 m and a second at 250-300 m (Fariña & Pereiro, 1995). In the Adriatic Sea (Mediterranean), the seasonal shift in preferred depth was less pronounced and maximum abundances during winter were shallower (~30 m) than during spring surveys (~50 m) (Figure I-4).

I-4. *LIOCARCINUS DEPURATOR* SPATIAL STRUCTURE

Scuba diving observations indicate that *L. depurator* migrates (Glass, 1985). The crabs tended to be aggregated and were found within 1 m from each other (Glass, 1985). Glass (1985) suggested that this behaviour is associated with feeding and anti-predatory behaviours.

Freire *et al.* (1991b) and González-Gurriarán *et al.* (1993) off the Atlantic Iberian coasts and Ungaro *et al.* (1999b) in the Southwest Adriatic Sea used geostatistical techniques to show that *L. depurator* could be found in patches of roughly ~18-22 km diameter on the Atlantic coast but between 70-160 km diameter in the Adriatic (converted using the formula 0.48° * 60 min * 1.852 km = 53.34 km, which for the exponential model used in that study, the effective range = 3 * range (Cressie, 1991): 53.34 km * 3 = 160 km) in autumn and 70 km (as before: 0.209° * 60 min * 1.852 km * 3 = 69.67 km).

González-Gurriarán *et al.* (1993) suggested that depth limited large-scale distribution of *L. depurator*, while upwelling, outwelling (nutrient rich waters from the Rías) processes and bottom sediment type affected the small scale distribution. In the Ría Ferrol, *L. depurator* was found in patches of 2-3.5 km and its distribution was determined by estuary salinity gradient at a large scale and by environmental fluctuations in more fluvial zones at a small scale (Freire *et al.*, 1993).

I-5. DISTRIBUTION IN RELATION TO HABITAT

Abele (1974) considers that the diversity of substrata is the most important factor determining decapod diversity (i.e. number of species). Almaça (1985) considered that depth and/or substrata are the major factors limiting competition of Mediterranean Brachyura. *L. depurator* possibly avoids competition from other *Liocarcinus* secies by occupying deeper habitats with muddy bottoms, preferentially (Almaça, 1985). For example, in the shallow Ría de Arousa (Galicia) there may be an overlap in distribution with *L. arcuatus*. However, *L. arcuatus* occupies sandy bottoms while *L. depurator* occupies mainly muddy areas (Muiño, 1997). In a Italian estuary, Minervini *et al.* (1982) found that *Liocarcinus depurator* occupied predominantly the muddy areas of the estuary whereas *Liocarcinus vernalis*, inhabited the sandy areas, over a depth range of 0-50 m.

Table I-1 shows the diversity of bottom substrata where *L. depurator* has been found. Muddy sediments are by far the most common.

Table I-1: Substrata where *Liocarcinus depurator* is found throughout its geographic range.

Depth (m)	Substrate	Area	Reference
5-256	Sand/mud/detritus	Adriatic Sea	Števcic, 1979; Števcic, 1990
80	Sand	Malta and Fifla Islands	Schembri & Lanfranco, (1984)
5-871	Muddy	Helenic Islands	d'Udekem d'Acoz, (1992)
3-871	Muddy	Catalan Coast	Abelló, (1993)
1-450	Sandy/ muddy	South Spain	González-Gordillo *et al.*, (1990); García-Raso, (1984)
10-750	Muddy	Ligurian Sea	Relini *et al.*, (1986)
10-600	Muddy	Ionian Sea	Pastore *et al.*, (1998)
90-135 350-650	Muddy; with *Funiculina quadrancularis*	Southern Sardinia	Manning & Froglia, (1982); Mura, (1987); Mura & Cau, (1994); Mura & Cau, (1992)
167-205	Shell remains	Marocco	García-Raso, (1996)
100-500	Shell remains with/without rock, rocky and muddy	Cap Bretón (Northwest France)	Díez *et al.*, (1994)
5-30	Coarse (high hydrodynamism)	Strait of Messina	Spanò, (1998)
80	Mud-sand	Portugal	Nunes-Ruivo, (1961)
0-450	Soft, sandy and mixed bottoms, gravel	British coast	Hayward *et al.* (1993)
12-40	Mud, sand, gravel and shell debris	Irish Sea (Anglesey)	Ramsay *et al.*, (1998)
65	Muddy	Sicilian channel	Falciai, (1997)
0-800	Mud, sand and detritus	Sicily	Pipitone & Arculeo (2003)

Liocarcinus depurator is also present on sandy substrata, but much less commonly. Minervini *et al.* (1982) found *L. depurator* distribution in the Tiber estuary to be negatively correlated with the percentage of sand in the sediment over a depth range of 10-50 m. This estuary had three types of substratum, clearly separated bathymetrically and geographically. The deepest with 1-30% of sand, the other with 30-60% of sand and the last and shallowest with 60-100% of sand (particle diameters between 0.5 mm and 0.05 mm) in relation to mud (particle diameters smaller than 0.05 mm) (Minervini *et al.*, 1982). In the Gulf of Gascogne (from Cap Michicaco to La Rochelle, 1964 to 1968), Lagardère (1973) found that *L. depurator* was 'common' or 'very common' in fine sediments, from 50 to 150 m depth, but was commonest in mid-range sediments at depths 100-150 m (Table I-2).

Table I-2 Density of *Liocarcinus depurator* according to the substrate type and depth interval in the Gulf of Gascogne (data from Lagardère, 1973). No information on the values (present, common or very common) was given in the original ref.

Depth	Gravel	Coarse sand (315-800 µm)	Fine sand (125-315 µm)	Very fine sand (50-125 µm)
0-50				Present
50-100		present	common	Present
100-150		present	very common	Common
150-200			present	

Pipitone & Arculeo (2003) found that *L. depurator* occurred in 12 out of 16 studied areas which were muddy, in Sicily. No *L. depurator* were found in the rocky areas, *Posidonia oceanica* beds, artificial reefs, fine sand or strictly sandy areas (Pipitone & Arculeo, 2003). Figure I-6 shows L. *depurator* density according to the substratum type in the North and central Adriatic Sea. It was found that crab density was greater in sand-silt-clay substrata.

Figure I-6: Average abundance of *Liocarcinus depurator* in the Northern-Central Adriatic sea, in the different sampled substrata (N from left to right =10, 13, 24, 26, 10, 12, 2, 3). Data from 46 and 54 hauls of bottom trawl surveys, during winter and spring of 1982, respectively (data from: Šimunovic, 1997).
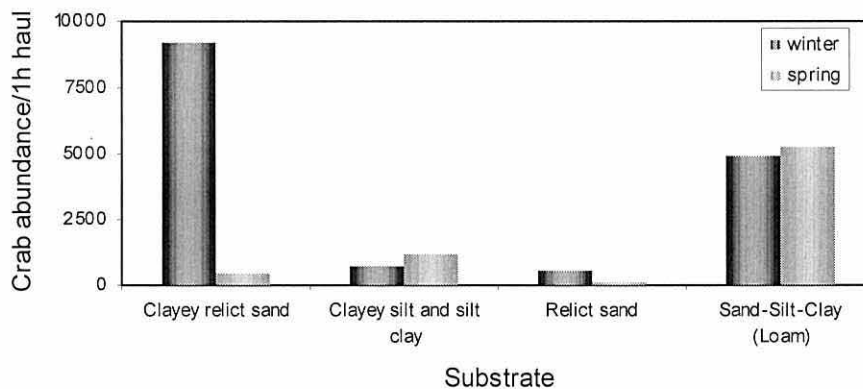
I-6. INTER-SPECIFIC RELATIONSHIPS IN DISTRIBUTION

The presence of similar potentially competing species, which occupy similar habitats with similar needs determines species abundance and distribution. *L. holsatus*, which in distribution ranges from the south of Iceland (Stephensen, 1939 in d'Udekem d'Acoz, 1999) to Cascais (Central Portugal)(Neves, 1967 in Almaça, 1985), also prefers muddy/sandy habitats and is a benthic scavenger (Groenewold & Fonds, 2000; Rees *et al.*, 1999). Like *L. depurator*, *L. holsatus* feeds on polychaetes, bivalves, echinoderms, crustaceans and juvenile fish, and

actively scavenges on dead fish and molluscs (Groenewold & Fonds, 2000). *L. holsatus* is more tolerant af low salinity, thus can be found further up in the estuaries than *L. depurator*. Abelló *et al.* (Abelló *et al.*, 1991) considered that these two species are expected to have a high degree of competition, in the areas where they coexist. These authors found that *L. depurator* showed maximum activity during the night whereas *L. holsatus* was the most active during the day, thus limiting potential competition (Abelló *et al.*, 1991).

Figure I-7: Percentage of occurrences (positive hauls) of *Liocarcinus depurator* (dark grey bars), *L. holsatus* (black bars) and *Macropipus tuberculatus* (light grey bars) in the areas where at least two crab species coexist. North Sea and Irish Sea were beam trawl samples, whereas Galicia was sampled by bottom trawl. Only 'cases' where the two species occurred were represented, i.e. in the Irish sea, the data is from the *Pleuronectes platessa–Limanda limanda* assemblage and in Galician shelf is from spring surveys. Data from, North Sea: Jennings *et al.* (1999); Irish Sea (*Pleuronectes platessa–Limanda limanda* assemblage): Ellis *et al.* (2000); Cap Bretón: Rallo *et al.* (1993); Galicia: Fariña *et al.* (1997); South of Portugal: Monteiro *et al.* (2001); Western Mediterranean: Abelló *et al.* (2002).
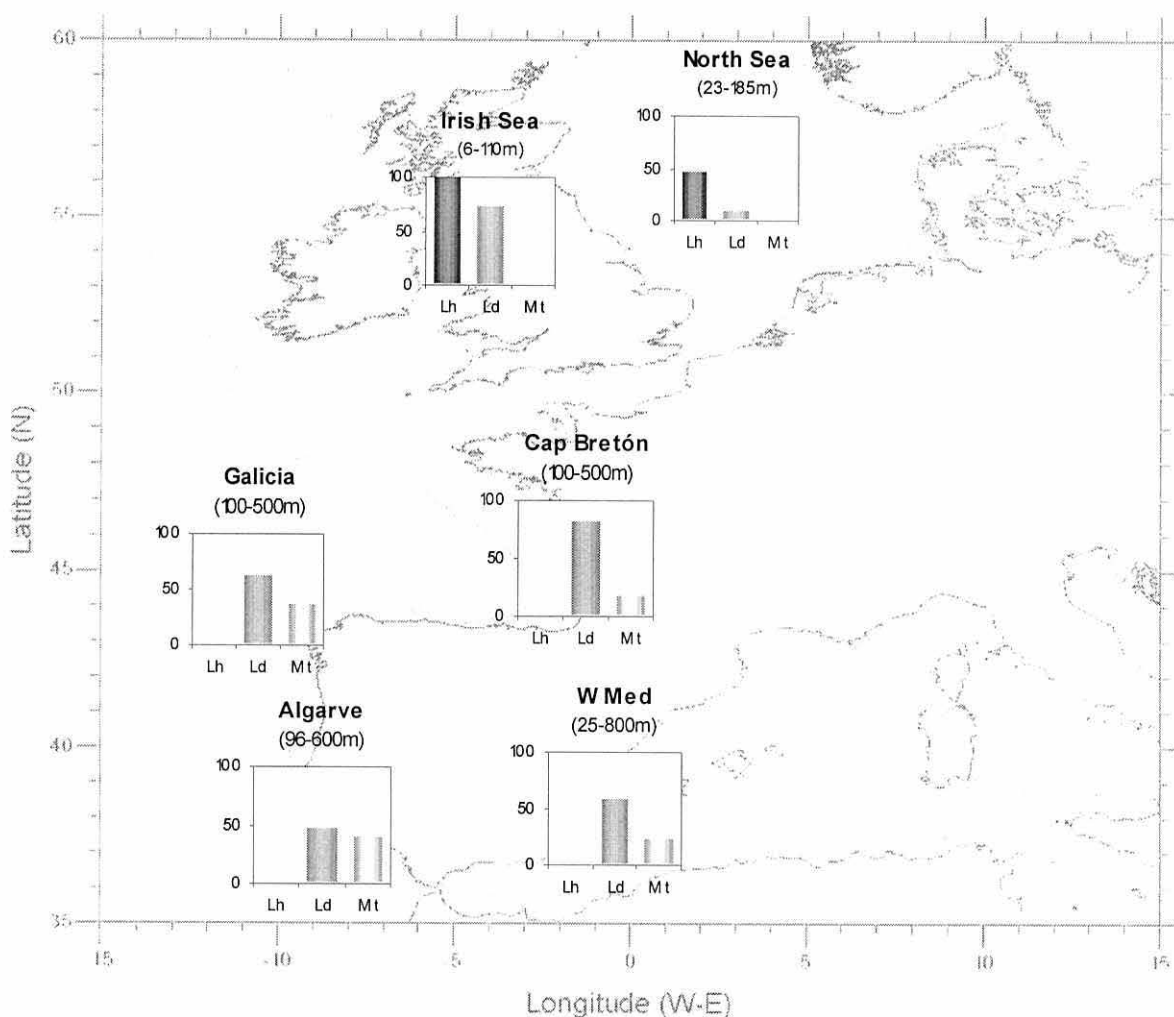
Liocarcinus holsatus, is much more abundant in the North Sea than *L. depurator* (Figure I-7). In a beam trawl study in the North Sea, *L. depurator* was found in 9.5% of 62

samples whereas *L. holsatus* was present in 47.9%. *L. holsatus* was the fourth most abundant species in the southern part of the sampling area (Jennings *et al.*, 1999). Around England and Wales, *L. holsatus* was among the six most numerically abundant species, occurring in 47% out of 69 beam trawl samples, (Rees *et al.*, 1999), and in the Irish Sea *L. holsatus* occurred in 80% of 101 beam trawls from 6 to 110 m whereas *L. depurator* occurred in only 3% (Ellis *et al.*, 2000) (Figure I-7).

On the Galician shelf, *L. depurator* occurred in 62% of the 168 bottom trawl samples during spring and in 59% of 293 hauls during autumn, while *L. holsatus* only occurred in 0.6% of the hauls, during Spring (Fariña *et al.*, 1997), from 100 to 500 m depth (Figure I-7).

In the Mediterranean coastal waters of Spain, *L. holsatus* did not occur during 9 years of bottom trawl surveys from 25 to 800 m depth (Figure I-7).

Figure I-7 appears to indicate that in the North Sea, *L. holsatus* restricts the densities and occurrences of *L. depurator* at shallower depths. In the Atlantic coastal waters of Spain and France, and in the Mediterranean, *Macropipus tuberculatus* potentially competes in deeper waters (Figure I-7). *M. tuberculatus*, also prefers muddy habitats and has similar feeding habits and has similar dimensions to *L. depurator*. *M. tuberculatus* was found from 51 to 700 m depth, with maximum occurrences observed from 200 to 400 m off the Mediterranean coast of Spain (Abelló *et al.*, 2002) (Figure I-8). Thus, *M. tuberculatus* coexists with *Liocarcinus depurator*, but its preferred depth range is deeper and abundances are much lower (Abelló *et al.*, 2002) (Figure I-8). In the Southern Adriatic Sea, the differences between abundances of both species decrease as *M. tuberculatus* becomes more abundant than *L. depurator* from 201-500 m (Ungaro *et al.*, 1999a) (Figure I-8).

Figure I-8: Left graph: Bathymetric variation of the percentage occurrence of *Liocarcinus depurator* (dark bars) and *Macropipus tuberculatus* (light bars) along the Mediterranean coast of Spain (Abelló *et al.*, 2002) and average abundance of both species (continuous line with triangles, *L. depurator* and *M. tuberculatus* (dashed line with the circles)) along the Catalan coast (data from: Abelló *et al.*, 1988). Right graph: Bathymetric average abundance (crabs.1h haul) of *Liocarcinus depurator* (black lines with triangle) and *Macropipus tuberculatus* (grey lines with the circle) along the Mediterranean coast of Italy (continuous lines) and Albania (dashed lines) and in the Southern Adriatic Sea (data from: Ungaro *et al.*, 1999a).
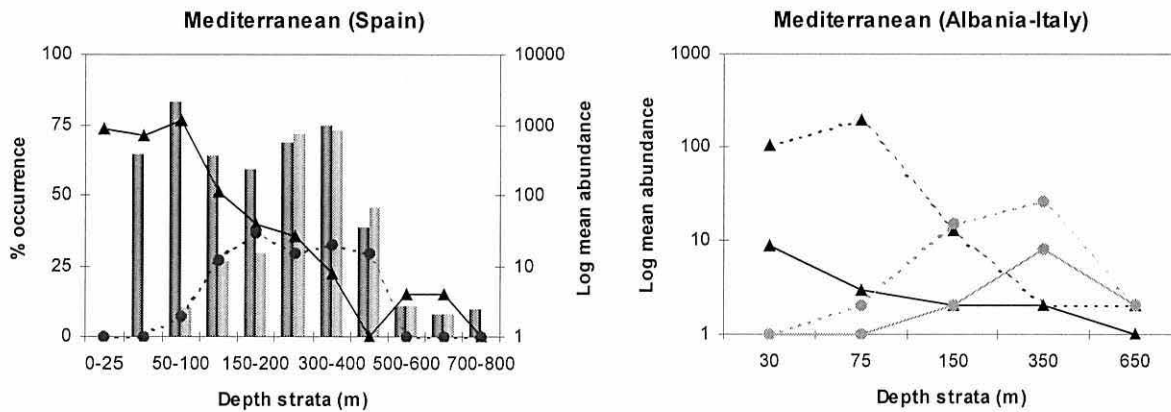
I-7. EFFECTS OF FISHING

Mortality due to fishing pressure of non-target species such as *L. depurator* occurs both by direct discard of non-commercial species/sizes from the fishing boats and through damaged the crabs by the fishing gear (non-catch mortality). In the latter case, damaged animals remain on the seabed and constitute an accessible food source. Demestre *et al.* (2000) have suggested that *L. depurator* aggregate in areas of high trawl disturbance. Bergmann *et al.* (2001) studied the damage to *L. depurator* in the Clyde sea Norway lobster fisheries, and Bergman *et al.* (2001) observed the survival of of this species after damage by fisheries.

Beam-trawled *Liocarcinus depurator* often have cracked or crushed carapaces and missing or broken appendages resulting in death within 48 h (Kaiser & Spencer, 1995). This damage is caused by the trawl chain mat and is not incurred within the cod end (Kaiser & Spencer, 1995). Ramsay *et al.* (1998) accessed the effect of non-catch mortality on *L. depurator* in three different areas within the Irish Sea. Off Dulas Bay-Anglesey (40 m, coarse sand) and in Red Wharf Bay-Anglesey (12 m, sandy) there was no significant effect on *L. depurator* density after trawling. However, in Walney Island (36 m, muddy) there was a significant decrease in density after two days of fishing (Ramsay *et al.*, 1998). Walney Island mud was clearly a preferred habitat for *L. depurator* hence it is not surprising to find greater or even significant impact where the densities were higher (Table I-3).

Table I-3: Summary of previous information on *Liocarcinus depurator* distribution and abundance. * indicates mean value calculated from the article and ? indicates when the information was not totally clear.

Ref.	Local	Abundance	Date	Depth range	Substrate/assemblage	Method	Number
(Sardà *et al.*, 1982)	Huelva-Cadiz (Spain)	1-10 crabs.h haul 1-10 crabs.h haul	01/02/1981	52-604	n.s.	Bottom trawl	33 hauls
(Ungaro *et al.*, 1999a)	Albania Italy	2.4 crabs.h haul 62 crabs.h haul	1996-1997	10-800	n.s.	Bottom trawl	40 hauls.2 years 72 hauls.2 years
(Ellis *et al.*, 2000)	Irish Sea (UK)	n.s. n.s. n.s.	Sep-98	6-110	*Pleuronectes platessa– Limanda limanda* assemblage *Nephrops norvegicus–* *Alcyonium digitatum*	Beam trawl	45 hauls 4 hauls 5 hauls
(Manjón-Cabeza & García Raso, 1998)	Cadiz (Spain)	4.8* crabs??	Oct-1993 to Sep-1994	15-24	coarse sand and fine gravel	Rock dredge	4 transects.month^{-1}
(García-Raso & Majón-Cabeza, 2002)	Cadiz (Spain)	2.5* crabs.??	Nov-1994 to Aug-1995	15-24	coarse sand and fine gravel	Rock dredge	4 transects.month^{-1}
(Lagardère, 1973)	Gulf de Gascogne (France)						
(Díez *et al.*, 1994; Rallo *et al.*, 1993)	Cap Bretón-near Biarritz and San Sebastian (Atlantic France)	0.77* crabs.10 min dredge 16.8* crabs.30' hauls	Jul-89	100-500	canyon	Rock dregde Bottom trawl	22 6
(Politou *et al.*,)	Ionian Sea (Greece) Argosaronikos (Greece)	10 crabs.h 11 crabs.h 5 crabs.h 10 crabs.h	summer 1996 summer 1997 summer 1996 summer 1997	10-200		Bottom trawl	41 40

(Table I-3 cont.)

Ref.	Local	Abundance	Date	Depth range	Substrate/assemblage	Method	Number
(González-Gordillo *et al.*, 1990)	Huelva-Cadiz (Spain)	11* crabs.sample	Dec-1988 to Oct-1989	0-20		Trawl, dredges, hand	27 samples
(Nickell & Moore, 1991)	Little Cumbrae Island (UK)	1.3* crabs.sampled month	Jan-1983 to Feb-1984	113	muddy sand	Creel	5 large+5 small
	Clach Station (UK)	5.9* crabs.sampled month		see article	hard sand		
(Cartes *et al.*, 1994)	Catalan Sea (Spain)	32 crabs.h haul	Autumn-winter 1991	146-296	shelf-slope	Bottom trawl	44+6 hauls
		8.4 crabs.h haul		245-485	upper slope		
		3.5 crabs.h haul			upper slope		
		1.4 crabs.h haul		430-515	canyon		
(Olaso, 1990)	Cantabrian Sea (Spain)	38* crabs.30 min haul	Spring 1983-1987	0-800		Bottom trawl	135
		77* crabs.30 min haul	Autumn				149
(Ramsay *et al.*, 1998)	Anglesey-Red Wharf Bay (Wales)	0-20 crabs.1000 m2	1995	12	medium sand	Beam trawl	6
	Anglesey offshore (Wales)	0-10 crabs.1000 m2		40	coarse sand with gravel and shell debris		6
	Walney Island (Wales)	20-70 crabs.1000 m2		36	muddy		6
(Fariña *et al.*, 1997)	Galicia (Spain)	30.94 crabs.30 min haul	Autumn (1980-86)	100-500		Bottom trawl	293
		48.88 crabs.30 min haul	Spring (1984, 86, 87)				168
(González-Gurriarán *et al.*, 1995)	Ría de Arousa (Spain)	119.8* crabs.10 min haul	Apr-89	10	raft area (muddy)	Beam trawl	4
		207* crabs.10 min haul		20	raft area (muddy)		4
		10.6* crabs. 10 min haul		40	middle channel (muddy)		4

(Table I-3 cont.)

Ref.	Local	Abundance	Date	Depth range	Substrate/assemblage	Method	Number
(González-Gurriarán, 1986)	Ría de Muros e Noia (Spain)	23* crabs. 10 min haul	Oct-1978 to Jul-1979	15	raft area (muddy)	Semi-ballon trawl	2
		100.2* crabs. 10 min haul		15-40	middle channel (muddy)		6
		10.2* crabs. 10 min haul		2-6	beach (sandy)		6
(Freire et al., 1993; González-Gurriarán et al., 1991)	Ría de Ferrol (Spain)	1.87* ind.10 min tow	Sep to Oct 1990	1-32		Beam trawl	35
Prelimiry estimates in Hall et al. (1990a)	Loch Gairloch, (Scotland)	13-14 juvenile.m-2	1987 (?)	5-10 m	sandy bottom	Visual sensus (?)	
		0.25 adults.m-2					
(Glass, 1985; Glass & Huntingford, 1988)	Loch Sween (Scotland)	0.04 crabs.m- 2	Feb-1981 to Jun-1982	-		Scuba	
(Basford et al., 1989)	Northern North Sea (Scotland)	0-10 crabs.1000 m-2	1980-84	0-200		Agassiz trawl	152
(Gaspar et al., 2003)	Sines-Lagoa de Santo André (Portugal)	3.3 crabs/5 min dredge	Jun-01	8-10	sandy (bivalves)	North dredge	12
		24.6 crabs/5 min dredge				Traditional dregde	12
		12.5 crabs/5 min dredge				grid dredge	12
(Crothers, 1969)	Milford Haven-Bay Roads	0.1* crabs.bait	Jul-1964 to Sep-1966	0->10	muddy-sand	Baited traps	255
(Šimunovic, 1997)	Northern Adriatic	952.9* crabs.h haul	Apri-May 1982	12-396		Bottom trawl	46
		2957.* crabs.h haul	Nov-Dec 1982	12-420			54

I-8. OBJECTIVES OF THE THESIS

I- 8.1. Part I: Distribution of *Liocarcinus depurator* in the western Mediterranean coast of Spain: small and large scale approaches.

There are a number of approaches which have been taken to examine the distribution of a species once the density measurements from a sampling programme have been made. The different approaches provide different sorts of information (e.g. maps of density, modelled trends) and may result in different interpretations. Bottom trawl time series are becoming increasingly common, but these are generally based on too few years for adequate periodicity measurements although they can still provide important information on the population's temporal evolution.

The simplest approach taken to analyse species distribution has been to study the sources of variation separately. The spatial component can be considered as the average density for defined segments of coastline within a graded series of depth ranges. The temporal component is then superimposed. Differences between grouped samples from each sector, depth interval or year can be considered separately by subsuming the variation from other components in the analysis of a single factor. More appropriate is the factorial approach whereby geography, depth and time are considered together and their contributions to the variation in density estimated prior to comparisons between levels of factors.

However, the factors that influence the abundance of *L. depurator* are unlikely to coincide with human perceptions of depth bands or consistently located geographic pieces of coast. The result of such add-hoc amalgamation of replicates into regional samples is almost always to inflate the variability within factors to an unacceptable level. Depth, geography and time vary in a continuous manner and any analysis of spatial and temporal data should acknowledge this fact and not hide its variability behind means, medians and confidence intervals for discontinuous factors.

Thus, to take into account this geographic, bathymetric and temporal continuity, two main approaches were considered, one based on linear models (LM) and another based on geostatistics. Both approaches are from a broad family of statistical models that relate a set of explanatory (or "independent" or "predictors") variables to a response (or "dependent") variable. In both cases, the set of independent variables can include space (latitude and longitude) but in geostatistics includes the auto-correlation function of the dependent variable. Thus geostatistics is based on the basic assumption that the data are autocorrelated in space, the closiest

the distance separating the points the more likely they are to share the same value. The second approach is based on the functional relationships between the observed data and the values of spatial, temporal or any other quantitative measures of divergence.

Both methods have been widely applied, although in both cases increased computation power and general awareness has led to increased use by marine biologists. Still, most studies do not consider both methods. Those two approaches may give different results, but may overlap in some degree.

In this thesis, first a general methodology where the survey details are extensively explained followed by an introduction to the oceanographic and geophysical characteristics of the sampled area (Mediterranean coast of Spain) are given. Then, using the same data set, each of the three approaches are applied. The advantages and disadvantages of these three main approaches to compare the results obtained by each of them are discussed in the current work.

Figure I-9: Summary of the approaches considered in the study of crab density distribution.
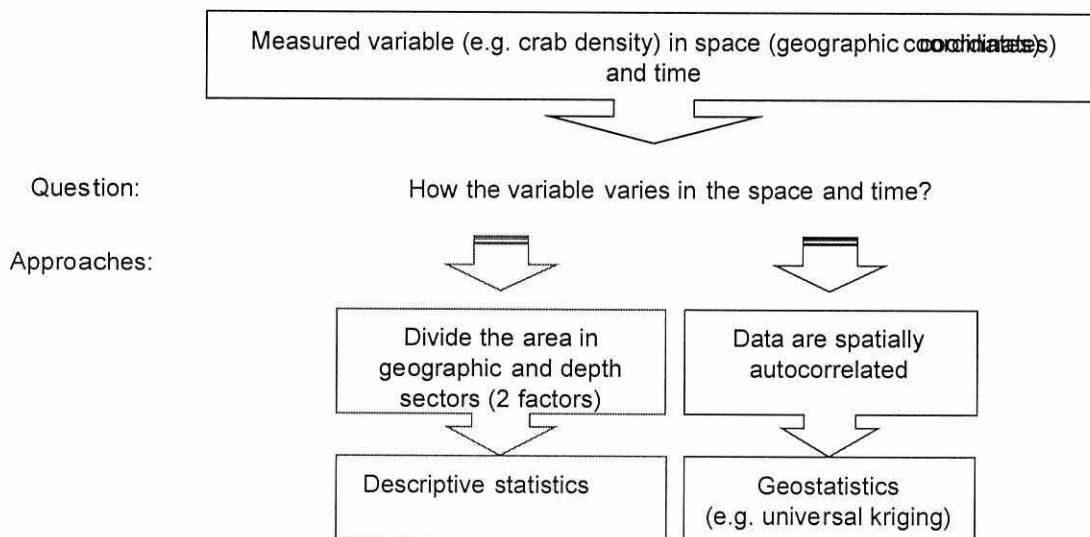
Preceding the geostatistical studies, a small introduction to the methodologies is given, which is followed by a work where different geostatistical methodological options are compared using the same data set. Additionally, the small scale spatial structure of *Liocarcinus depurator* distribution is studied in relation to environmental characteristics of the sediment, using geostatistical methodologies. One of the purposes of this thesis was to provide complete and comparable information on the results given by each approach, thus a researcher can choose according to the characteristics of the dataset and the purposes of its study, which

would be the most convenient methods to apply, in any particular case. Figure I-10 represents the sequence of part I, in the current thesis.

Figure I-10: Diagram of the first part of the thesis.

General Introduction

•Introduction to the surveys ⟶

•Introduction to the sampled area
(oceanographic characteristics) ⟶

Geographic, bathymetric and annual variation of *L. depurator* densities.

1. Descriptive statistics and univariate analysis ⟶

2. GLM and GAM ⟶

3. Geostatistics

• Introduction to geostatistics

• Review of geostatistics applied to crustaceans

• Effect of geostatistical options, in the spatial model and kriging estimates

• Geostatistical analysis of the *L. depurator* densities in the western Mediterranean coast, from 1994 to 2003. ⟶

• Geostatistical analysis of small scale *L. depurator* distribution. Relationships with sediment varables

I- 8.2. Part II: On the application of geometric morphometrics to the *Liocarcinus depurator* carapace

Variation in body shape can often reflect ecological and behavioural differences between organisms. The range of body shapes exhibited by a particular species is a result of countless evolutionary refinements and thus should accurately reflect a range of ecological, physiological and behavioural influences impinging on individuals. Crustaceans, with their hard exoskeletons, are excellent organisms for studying shape differences in relation to the physical and biological environment.

Body shape has been analysed traditionally, through linear measures (traditional morphometric analyses) where the use of bivariate or multivariate methods is applied to sets of variables (e.g. distances, angles, ratios). These methods have been widely used in Crustacea

ranging from studies of potential allometry to size correction and population dynamics. Recent advances have resulted in a new field of shape analysis called geometric morphometry, in which, for example, "landmark co-ordinates" are recorded in several dimensions to directly capture the geometry of the object (Rohlf, 1990).

Through geometric morphometry the shape, rather than the relative dimensions, of the individual is studied. Thus any differences found do not rely on a few linear measures (i.e. length, width or height), but on a detailed analysis of the shape. Another fundamental aspect of these new techniques is that they provide easy visualisation of the shape differences. Furthermore, the 'shape' variables produced can be analysed by multivariate statistical methods to determine the significance of differences in shape.

Crustaceans are an excellent group for applying geometric morphometry due to their hard exoskeleton and easily identifiable homologous landmarks. However, the application of geometric morphometry to crustaceans has been, to date, limited. Rosenberg (1997) studied the shape difference between the major and minor chelipeds in the fiddler crab *Uca pugnax* (Smith). The differences observed in the major claw were associated with the ability of producing more power, suggesting that selection for combat effectiveness has played an important role in the evolution of the major cheliped shape. The same author studied claw shape variation across the genus *Uca* (Rosenberg, 2002). Cadrin (2000; 1999) applied box-truss methods to discriminate sexes and fisheries stocks of the American lobster, *Homarus americanus*, based on size at maturity (Cadrin, 1995). The same author reviewed the use of morphometrics for the identification of fisheries stocks (Cadrin, 2000; Cadrin & Friedland, 1999).

Various aspects of the application of geometric morphometry to *Liocarcinus depurator* shape difference will be explored. The general applicability and limitations of the techniques will be highlighted in this thesis. In many studies, samples are collected and many are preserved for latter measurements. It is usually accepted without question that preservation will not produce significant changes to dimension or shape of the preserved material. However, the carapace width of the rock lobster, *Panulirus cygnus*, decreased significantly after freezing or boiling (Melville-Smith & Thomson, 2003). Mainly freezing, storing in alcohol or formaldyhyde preserves crustaceans. Often, samples have different origins and have been preserved through different techniques. It was tested if there was a significant shape difference between fresh material and that, which had been frozen or preserved in alcohol.

It has been widely known that males and females have significantly different sizes and growth curves. However, are these changes restricted to size, or there are further differences in the shape of each gender? Are there differences between male and female carapace shape? Is there any shape change in the carapace, during growth?

Figure I-11: Diagram of the second part of the thesis.

| Introduction to geometric morphometry methods. |

| Review of geometric morphometry applications in marine biology, particularly in crustacean studies. |

| Is there an effect of preservation, on shape? |

| Do males and females have different shapes? |

| Do animals from diverse geographic locations have different shapes? |
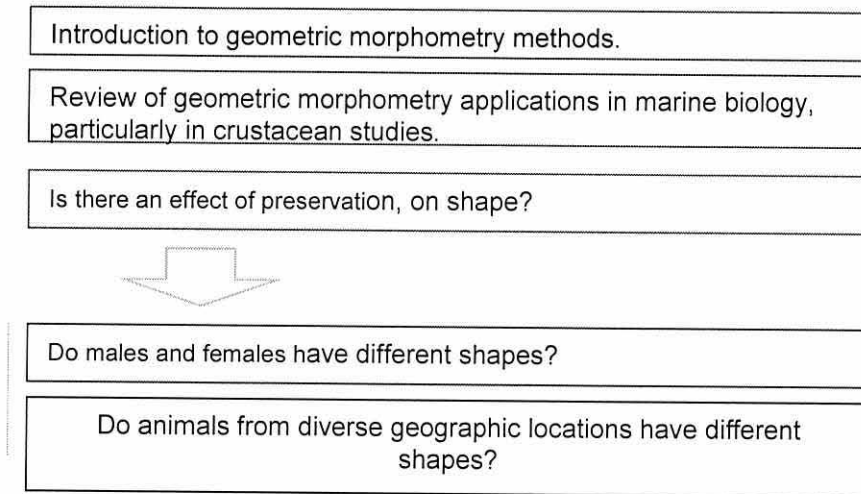
In the final part of the thesis, a general discussion integrates all the results found throughout the investigation (section XI).

PART I. Distribution of *Liocarcinus depurator* in the western Mediterranean coast of Spain: small and large scale approaches.

PREFACE

Global commercial production from fisheries and aquaculture is currently the highest on record and remains highly significant for global food security, providing more than 15 percent of total animal protein supplies (FAO-web resource). During 2000, 94.8 millions tons (representing 81 billions US$) of total commercial fishery production was recorded. EC marine fisheries landings during the same year were 7.24 million tones. In recent years there has been a growing awareness that the traditional approach to managing fisheries, which considers the target species as independent, self-sustaining populations, is flawed. It is being recognised that sustainable use of the world's living aquatic resources can only be achieved if both the impacts of the ecosystem on the living resources and the impacts of the fishery on the ecosystem are explicitly identified and, understood.

By-products of commercial fishing, 'Discards', are defined as marine fauna brought onto the deck of a fishing vessel and subsequently returned to the sea. Alverson & Hughes (1995) estimated average global discard to be 27 million tons (about 27% of the global catch). The reasons for discarding part of the catch vary from the simple, the species has no commercial value, to the complex, for example the individual is below the legal capture size or 'quotas have already been fulfilled. There is little doubt that 'discards' are usually damaged and rarely make a full recovery hence have a direct impact on the general 'health' of the fished locality.

II. Introduction to the surveys and characteristics of the Mediterranean coast of Spain

Part I of this thesis was performed using data sets obtained in two distinct surveys, GEODELTA and MEDITS-ES. The current chapter aims to introduce and the surveys the context in which they were conceived.

II-1. GEODELTA SURVEY

II- 1.1. Aims and protocol

Data from this project was kindly provided by Doctor Francesc Maynou and Doctor Francesc Sardà, in the form of a series of numerical measurements. The author of the current thesis perfomed the analysis.

The project was conceived to assess the application of geostatistics to stock estimation of *Nephrops norvergicus* (Norway lobster).

A trawl survey was conducted over muddy bottoms off the continental shelf and slope of the Ebro delta (40°20'N to 41°00'N, NE Spain, Figure II-1) using the Research Vessel "García del Cid". A regular grid of 1 × 2 nautical mile quadrats was established parallel to the coast. Each trawl was randomly ascribed a starting location within each quadrat. A few southerly quadrats were not sampled thus avoiding oil production platforms. Sampling was conducted between 7 and 15 April 1994 at a total of 72 stations. The water depth varied from 83 to 713 m across the sampled sites. The northern part of the study area was characterised by a narrow shelf (8-10 km wide) having a gentle slope seaward which is indented by deep submarine canyons. South of ~ 40°50' N, the shelf becomes progressively wider (38-40 km) and the slope becomes steeper with fewer submarine canyons. Samples were taken with a modified otter trawl, drawn by a single warp ('Maireta System Trawl', Sardà *et al.*, 1994). The codend stretched mesh width was 12 mm in order to retain small individuals not normally caught by commercial fishing gear. The working dimensions of the trawl mouth were measured acoustically (SCANMAR) and averaged 13.4 m across by 2.0 m high. The effective trawling time was 15 minutes and trawls were always made parallel to the depth contours. Towing speed varied between 2.3 and 2.7 knots (mean 2.5 knots). The surface area trawled on each tow was estimated from the GPS (initial and final position) and the SCANMAR (vertical oppening) readings.

Figure II-1: The GEODELTA project study area with the location of the sampling stations (crosses). The sites where sediment samples were also taken are marked with a circle. Contour lines represent depth isolines, from left to right, respectively, coast line, 50 m 100 m, 200 m, 400 m 600 m and 800 m depth. Grey area is a oil production platform exclusion zone.
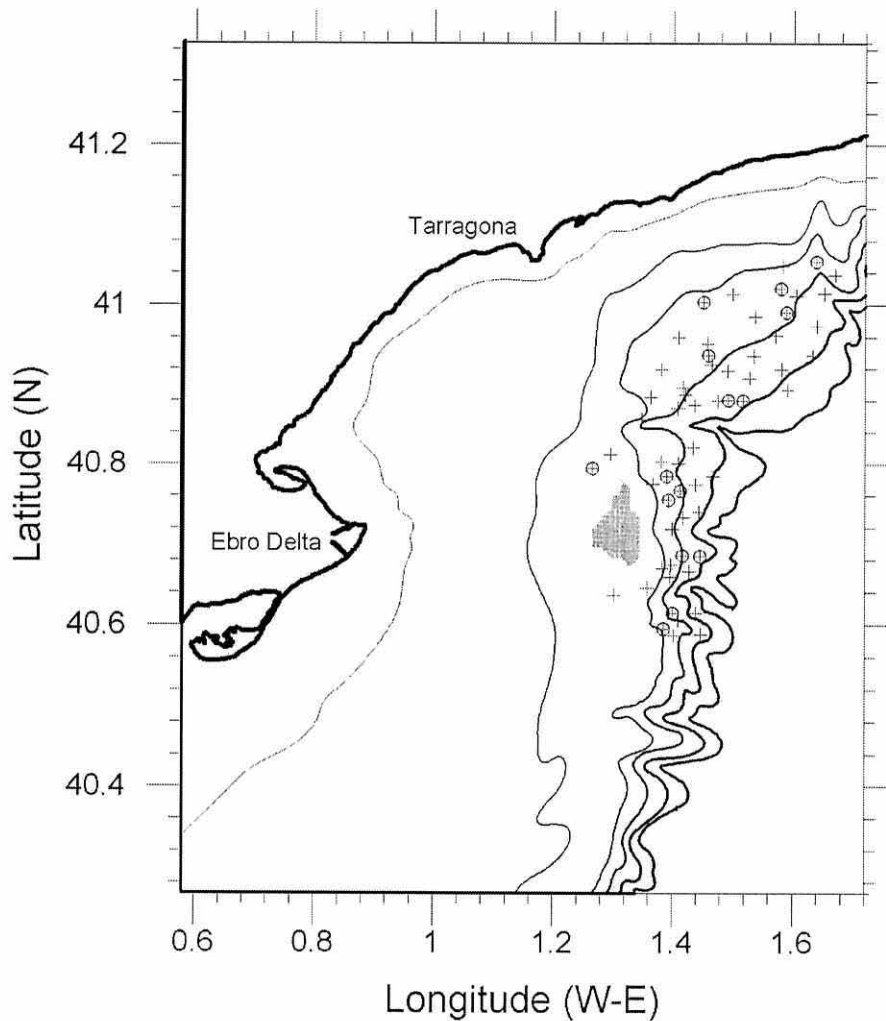
II- 1.2. Sediment variable measurements

Sediment samples were collected using a van Veen grab (Gray, 1981) on every second trawl, except on the continental shelf at depths shallower than 200 m, where sediment heterogeneity was presumed higher and the collection of one sediment sample per trawl was attempted. Sediment samples were analysed following the methodology presented by Maynou & Sardà (1997) and Alonso *et al.* (1999). The surface sediment temperature (T, °C) and the redox potential at 1 and 6 cm from the sediment surface (R1 and R6, mV) were measured on-board using a double-joint, multimeter electrode (Orion Research model 250A) immediately after the sample collection. Sediment samples were stored at −20 °C for later laboratory analyses. The redox potential is a measure of the lack of oxygen in the sediment and, in marine sediments, is usually negative with higher negative values for more reduced sediments. More

negative redox potential generally indicates sediments with higher quantities of organic matter. Normally, marine sediments are structured in layers when undisturbed, and deeper redox potential measurements generally show higher negative values than those near the surface. Grain size analysis was carried out on the sediment samples using a SEDIGRAPH 5000D for the fine-grained fraction (< 50 μm) and sedimentation tube analysis for the coarse-grained fraction. For each sample, the proportions of sand (62.5-1000 μm), silt (2-62.5 μm) and clay (0.06-2 μm) were determined. The grain size distribution of each sample was summarised by its median, $\varphi = -\log_2$ (median grain size in mm) (Gray, 1981), and its sorting coefficient IGSD (Inclusive Standard Deviation:Gray, 1981). Small values of IGSD indicate a well-sorted sediment and large values of IGSD indicate poorly sorted sediments (Maynou & Sardà, 1997). The carbonate content (% of CO_3 by volume) for each sediment sample was determined using a Bernard calcimeter, following the methodology presented by Vatan (1967).

II-2. MEDITS: MEDITERRANEAN BOTTOM TRAWL SURVEYS

II- 2.1. Aims and protocol

During the last decade, the need for a rationalisation of fisheries management in the Mediterranean has been highlighted. The MEDITS project was conceived to produce a common database of exploited demersal species within the Mediterranean area. This European Community project aims to provide measures of population distribution and demographic structure of benthic and demersal resources on the continental shelves and along the upper shelf slopes throughout the Mediterranean (Bertrand *et al.*, 2002). The programme detail was established with consideration of the outcomes from previous such programmes particularly that of the IBTS Group (ICES, 1992).

To ensure comparability, standardised sampling protocols were established and used by all participating countries. Thus common survey design, sampling gear and usage, information collected, and database management systems were employed throughout (Anon, 1998 in Bertrand *et al.*, 2002). Surveys were designed to cover all the accessible fishing areas over the shelves and upper shelf slopes, from 10 to 800 m depth, such that all the potential trawl fishing grounds were sampled (Bertrand *et al.*, 2002).

Trawl stations were distributed through stratified random sampling with strata delineated by depth contours (10, 50, 100, 200, 500 and 800 m). Each sample, however, ends up as a compromise between the constrains of random sampling and those of geostatistics (Green 1979 and Hilborn & Walters 1992 in: Bertrand *et al.*, 2002).

The envisaged sampling rate was one station per 60 square nautical miles, on average, in all areas, except the Adriatic Sea. Approximately the same trawl locations were visited every year. Throughout the Mediterranean about 1000 hauls are carried out during each annual survey.

The bottom trawl gear adopted was the GOC 73 (Fiorentini *et al.*, 1999), designed specifically for experimental fishing. The design represents a compromise enabling work at a wide depth range to be undertaken and an adequate range of species and individual sizes to be captured. The mouth opening is slightly higher than most commercial trawls (vertical opening 4 m rather than 3 and 2.5 m) which increases the range of species captured. The codend mesh size, 20 mm (stretched mesh), was smaller than commercial mesh sizes hence smaller specimens could be captured. Hauls performed at depths of less than 200 m had a duration of 30 minutes and those performed deeper, down to a maximum depth of 800 m, had a duration of 60 minutes.

With a few unavoidable changes, these surveys have been carried out at roughly the same time throughout the Mediterranean since 1994. Although the initial project was designed to survey specific target species, several countries opportunistically used the surveys to acquire extra information. Thus on the Spanish trawl surveys all the organisms in each haul have been identified, counted and often measured.

II- 2.2. MEDITS-es: Details of the Spanish survey

Data from this project was kindly provided by Doctor Pere Abelló and Doctor Luis Gil de Sola. The author of the current thesis participated in the surveys from year 2000 to 2003, and perfomed the data analysis.

The study area of MEDITS-ES encompassed the Spanish Mediterranean coast from Gibraltar to Cape Creus (Figure II-3). A bottom trawl survey performed with the research vessel 'Cornide de Saavedra' (Figure II-2) took place annually from 1994 to 2003 within the context of the MEDITS research programme framework (Bertrand *et al.*, 2002).

A total of 1098 successful trawls were taken, covering a total area of 45331 km^2 of the Mediterranean coast of Spain from 1994 to 2003 (Figure II-4). The number of hauls in each year, geographic sector and depth interval are presented in Table II-1, Table II-2 and Figure II-4). Between 77 and 134 hauls were performed per year, averaging around 110 (Figure II-4 and Figure II-5). All sectors were sampled over most of their area but Ibiza was poorly sampled (Figure II-4) and so excluded from subsequent analysis. The northern part of North Catalonia was not sampled in 1998. The Alborán island (located on the south of East Alborán

sector) area was only sampled in 1994 and 2000. The continental shelf in the Gulf of Vera is extremely steep and difficult to trawl hence the paucity (63) of hauls in that area. Furthermore, the excessive steepness of the continental shelf slope in the Ebro Delta meant that only the continental shelf was extensively sampled.

Figure II-2: Research vessel for the Spanish MEDITS survey.

Table II-1: Total number of successful trawls for each depth interval, year and sector taken around the Mediterranean coast of Spain from 1994 to 2003.

Depth	Hauls	Year	Hauls	Sector	Hauls
25-50	103	1994	77	EAlb	112
51-100	342	1995	106	WAlb	177
101-150	154	1996	105	Vera	65
151-200	55	1997	100	Alic	188
201-300	74	1998	92	Ibiza	38
301-400	80	1999	116	Vale	102
401-500	80	2000	111	Delta	188
501-600	101	2001	122	NCat	228
601-700	70	2002	134		
701-800	39	2003	135		

Figure II-3: Map of the MEDITS-ES project study area. Location of the MEDITS sectors are shown as programme codes on the left hand side and the finer resolution used in the current study shown on the right hand side. WALB: Western Alborán Sea, from Gibraltar to Nerja; EALB: Eastern Alborán Sea, from Nerja to Cape Gata; VERA: Vera Gulf, from Cape Gata to Cape Palos; ALIC: Alicante, from Cape Palos to Cape La Nao; IBIZ: Ibiza island; VALE: Valencia, from Cape La Nao to Castellón; DELT: Ebro Delta region, from Castelló to Tarragona and NCAT: North Catalonian, from Tarragona to Cape Creus
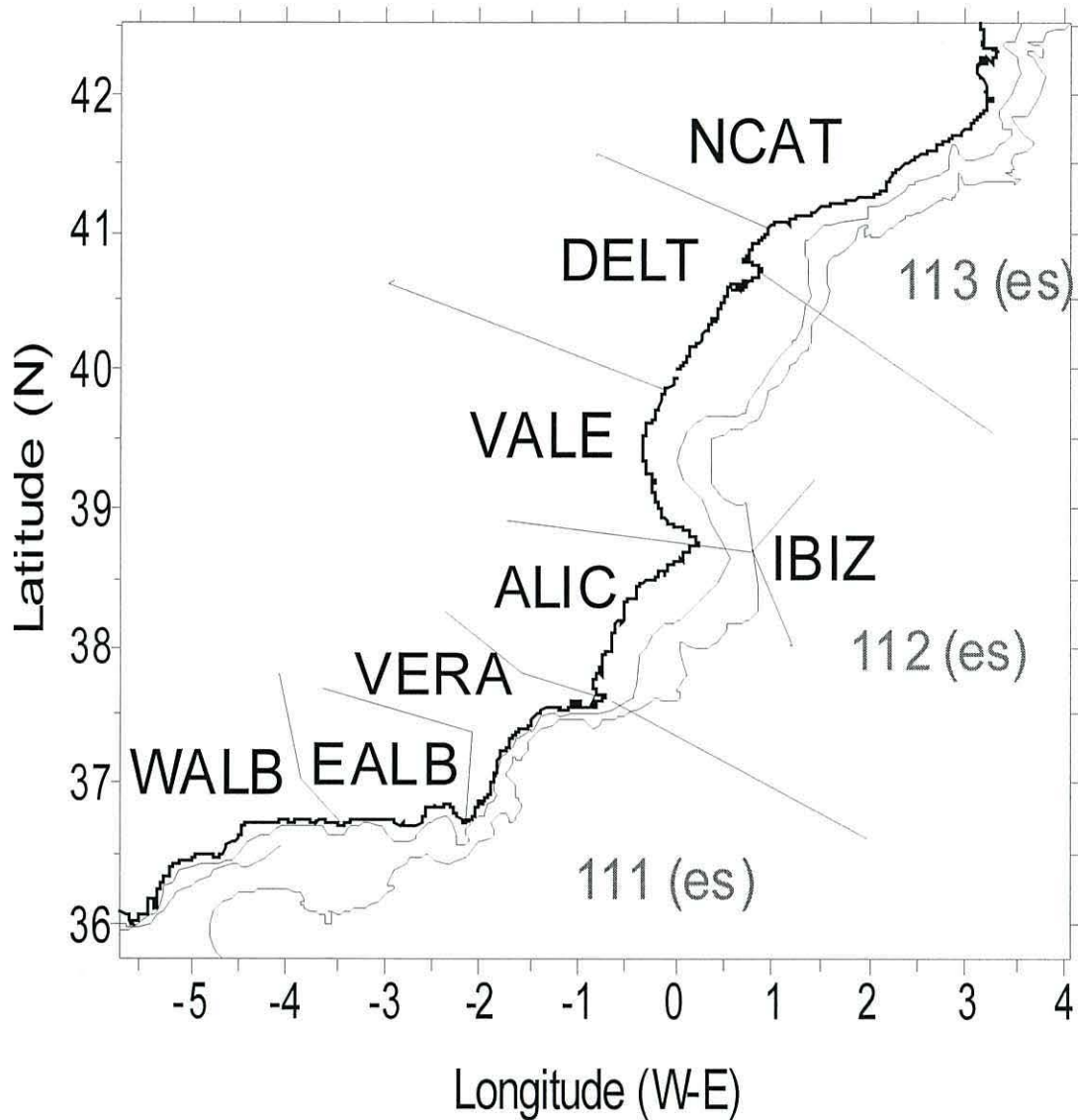
Figure II-4: Number of trawls, within the geographic areas and depth intervals. The years are represented by the colours in the stacked bars, from left to right, 1994 to 2003. WALB: Western Alborán Sea, from Gibraltar to Nerja; EALB: Eastern Alborán Sea, from Nerja to Cape Gata; VERA: Vera Gulf, from Cape Gata to Cape Palos; ALIC: Alicante, from Cape Palos to Cape La Nao; IBIZ: Ibiza island; VALE: Valencia, from Cape La Nao to Castellón; DELT: Ebro Delta region, from Castelló to Tarragona and NCAT: North Catalonian, from Tarragona to Cape Creus.
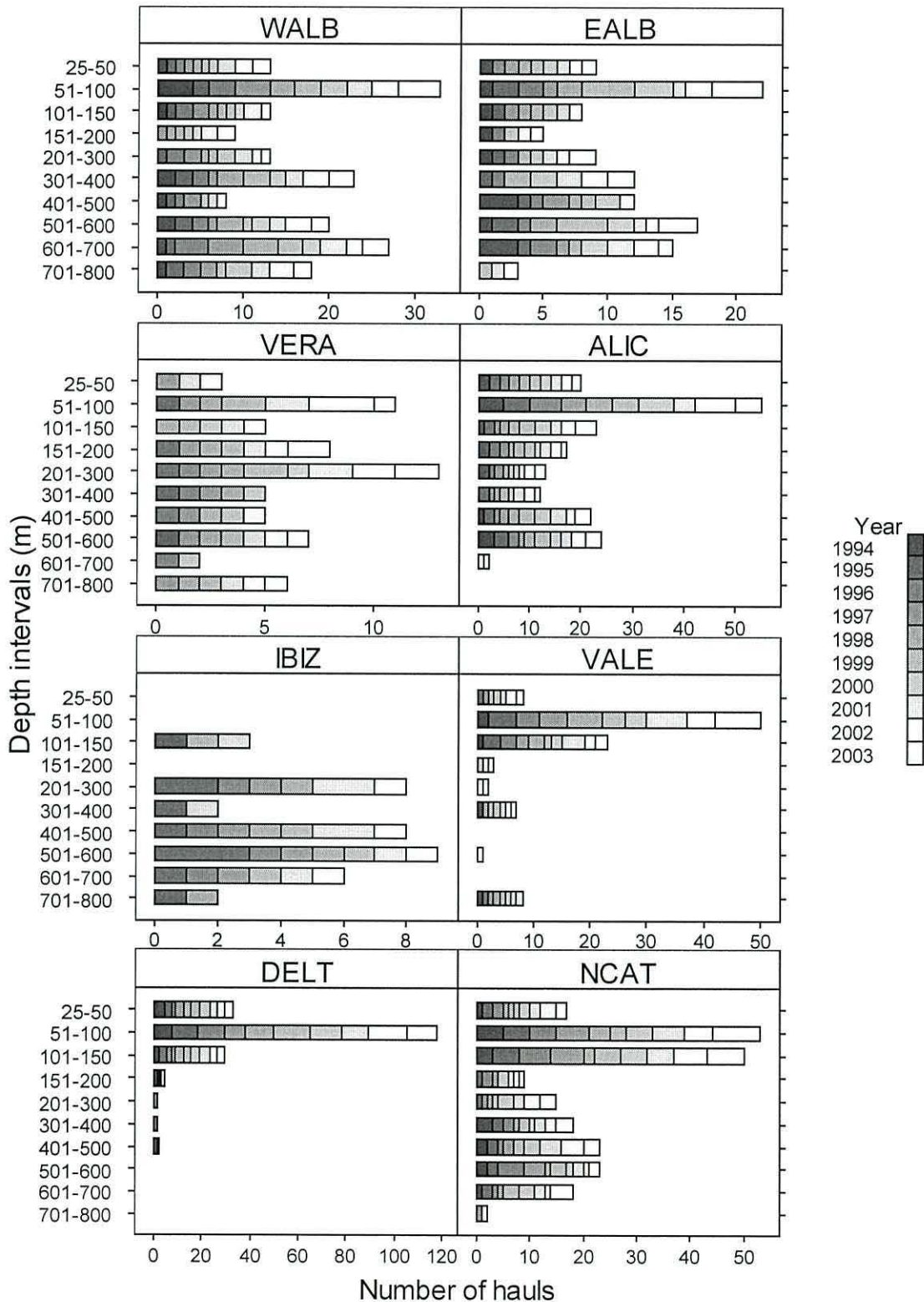
Figure II-5: Distribution of the MEDITS-ES sampling stations from 1994 to 2003. Contour lines represent the coast, 200 m and 1000 m depth. The geographic areas are labelled in the first figure (1994). The Balearic Islands have been omitted from the map for clarity. See Figure II-3 for the abreviations of the sectors. Each geographic sector is plotted with different symbols. Longitude scale refers to the first left bottom graph, the remaining graphs are repetitions with the same scale.
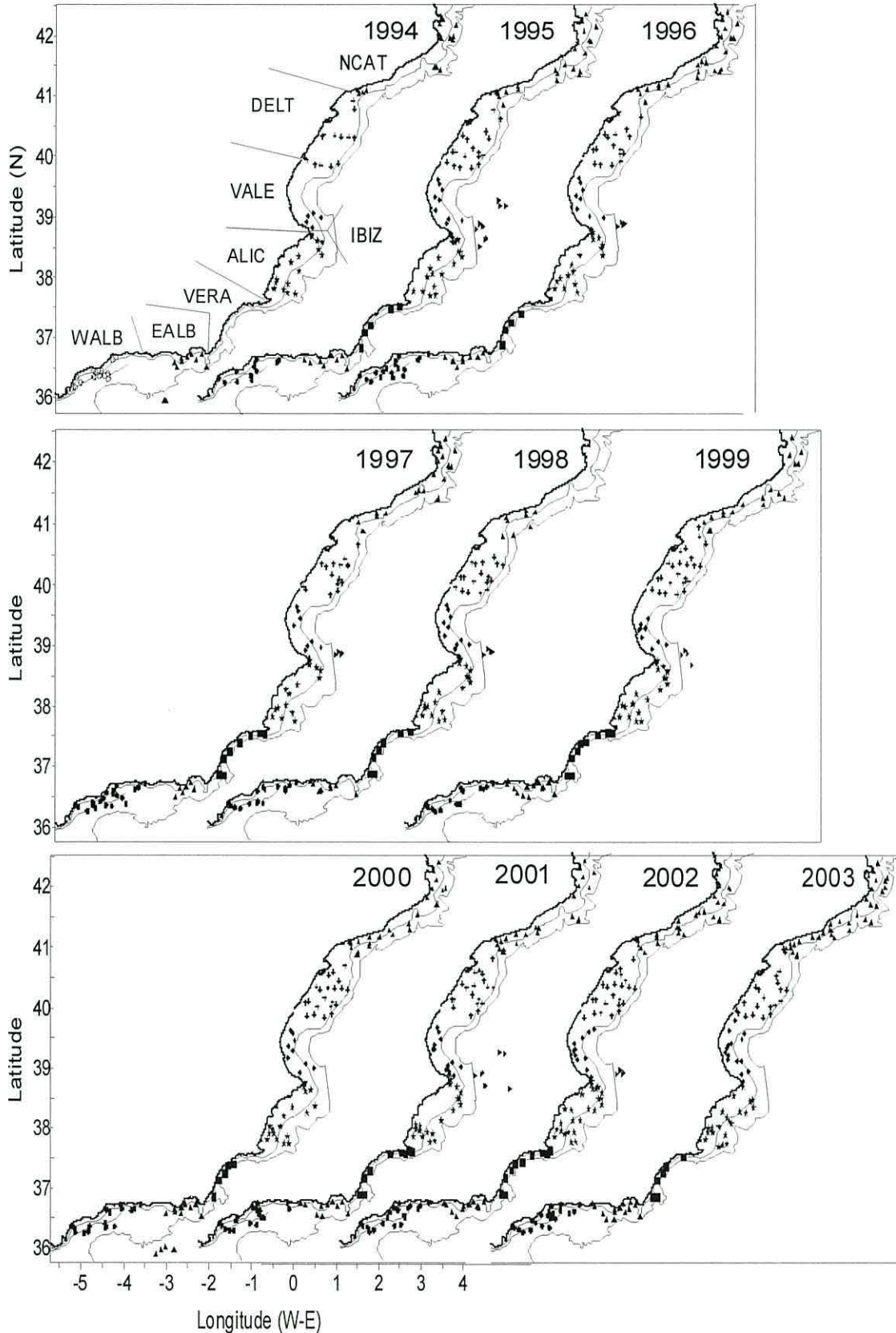
Table II-2: Number of hauls in MEDITS-ES per geographic sector, year and depth interval. Totals and sub-totals are presented in bold. See Figure II-3 for the abreviations of the sectors.

Year	Sector	25-50	51-100	101-150	151-200	201-300	301-400	401-500	501-600	601-700	701-800	Total
1994	WALB	1	4	1			2	1	2	1	1	**13**
	EALB	1	1	1	1	1		3	1	3		**12**
	ALIC	2	5	1	2	2		1	3			**16**
	VALE		2	1			1				1	**5**
	DELT	4	7	2	1							**14**
	NCAT	1	5	3			3	2	2	1		**17**
Total		**9**	**24**	**9**	**4**	**3**	**6**	**7**	**8**	**5**	**2**	**77**
1995	WALB	1	2	1		1	2	1	2	1	2	**13**
	EALB		2	1		1	1	1	2	1		**9**
	VERA		1		1	1	1		1			**5**
	ALIC	2	5	2	2	1	2	2	3			**19**
	IBIZ			1		2	1	1	3	1	1	**10**
	VALE	1	5	3							1	**10**
	DELT	3	11	3				1				**18**
	NCAT	2	5	5	1	1	2	2	2	2		**22**
Total		**9**	**31**	**16**	**4**	**7**	**9**	**8**	**13**	**5**	**4**	**106**
1996	WALB	1	3	2		2	2	1	2	4	2	**19**
	EALB	1	2		1	1	1	1	1	2		**10**
	VERA					1	1	1		1		**4**
	ALIC	2	6	1	2	2	1	1	2			**17**
	IBIZ					1		1	1	1		**4**
	VALE	1	4	3							1	**9**
	DELT	2	11	2			1					**16**
	NCAT	2	5	6	2	1	2	1	5	1	1	**26**
Total		**9**	**31**	**14**	**5**	**8**	**8**	**6**	**11**	**9**	**4**	**105**
1997	WALB	1	4	2	1	2	1	2	1	4	2	**20**
	EALB	1	1	1				2		1		**6**
	VERA	1	1		1	1	1	1	1		1	**8**
	ALIC	2	5	2	1	1	1	2	1			**15**
	IBIZ					1		1	1	1		**4**
	VALE		5	2			1				1	**9**
	DELT	3	9	2		1						**15**
	NCAT	1	6	6	1	1	1	2	4	1		**23**
Total		**9**	**31**	**15**	**4**	**7**	**5**	**10**	**8**	**7**	**4**	**100**

(Table II-2 cont.)

Year	Sector	25-50	51-100	101-150	151-200	201-300	301-400	401-500	501-600	601-700	701-800	Total
1998	WALB	1	3	1	1	1	3		3	4		17
	EALB	1	2	1				1	2	1		8
	VERA		1	1	1	1	1		1		1	7
	ALIC	2	5	2	2	1	2	2	2			18
	IBIZ					1		1	1		1	4
	VALE	1	6	3			1				1	12
	DELT	3	12	3								18
	NCAT	1	4	2					1			8
Total		**9**	**33**	**13**	**4**	**4**	**7**	**4**	**10**	**5**	**3**	**92**
1999	WALB	1	3	1	1	1	3		1	3	1	15
	EALB	1	4	1		1	2	1	4		1	15
	VERA		2	1	1	2		1	1		1	9
	ALIC	2	5	3	2	1	1	3	3			20
	IBIZ			1				1	1	1		4
	VALE	1	4	1	1		1				1	9
	DELT	4	15	3	1			1				24
	NCAT	1	3	5		1	2	2	3	3		20
Total		**10**	**36**	**16**	**6**	**6**	**9**	**9**	**13**	**7**	**4**	**116**
2000	WALB	1	3	1	1	2	2	1	2	2	3	18
	EALB	1	3	1	1	1	2	2	2	2		15
	VERA			1		1	1	1		1		5
	ALIC	2	7	3	1			3	2			18
	VALE	1	4	2			1				1	9
	DELT	4	13	4								21
	NCAT	2	5	5	2	3	1	3	1	3		25
Total		**11**	**35**	**17**	**5**	**7**	**7**	**10**	**7**	**8**	**4**	**111**
2001	WALB	2	3	1	1	2	2	1	2	3	2	19
	EALB	1	1	1		1	2		1	2	1	10
	VERA	1	2	1	1	2			1		1	9
	ALIC	2	4	2	2	1	2	3	2	1		19
	IBIZ			1		2	1	2	1	1		8
	VALE		7	4		1					1	13
	DELT	3	11	4								18
	NCAT	2	6	5	1	2	2	4	2	2		26
Total		**11**	**34**	**19**	**5**	**11**	**9**	**10**	**9**	**9**	**5**	**122**
2002	WALB	2	3	2	2	1	3		3	2	3	21
	EALB	1	2	1	1	1	2	1	1	2		12
	VERA	1	3	1	1	2		1	1		1	11

(Table II-2 cont.)

Year	Sector	25-50	51-100	101-150	151-200	201-300	301-400	401-500	501-600	601-700	701-800	Total
	ALIC	2	8	3	2	2	2	2	3	1		**25**
	IBIZ					1		1	1	1		**4**
	VALE	2	5	2	1		1					**11**
	DELT	3	16	3	1							**23**
	NCAT	3	5	6	1	3	2	4	1	1	1	**27**
Total		**14**	**42**	**18**	**9**	**10**	**10**	**9**	**10**	**7**	**5**	**134**
2003	WALB	2	5	1	2	1	3	1	2	3	2	**22**
	EALB	1	4		1	2	2		3	1	1	**15**
	VERA		1		2	2			1		1	**7**
	ALIC	2	5	4	1	2	1	3	3			**21**
	VALE	1	8	2	1	1	1		1			**15**
	DELT	4	13	3	1							**21**
	NCAT	2	9	7	1	3	3	3	2	4		**34**
Total		**12**	**45**	**17**	**9**	**11**	**10**	**7**	**12**	**8**	**4**	**135**
Total all		**103**	**342**	**154**	**55**	**74**	**80**	**80**	**101**	**70**	**39**	**1098**

Figure II-6 shows that sampling took always place in late spring, early summer (May-June in general). The latest surveys were those of 1994 and 2000, which ended on the 19th and 23rd June, while the earliest were those of 1995 and 2003, which started on the 22nd and 24th of April respectively. The difference between the earliest sampling and the latest sample date is two months (1995 and 2000, see Table II-3).

Table II-3: Start and end dates of the surveys also showing the depth ranged sampled, each year.

	date		Depth	
year	start	end	min	max
1994	28/05/94	19/06/94	27	786
1995	22/04/95	21/05/95	25	771
1996	02/05/96	27/05/96	27	779.5
1997	10/05/97	03/06/97	26.5	761
1998	03/05/98	30/05/98	25.5	726.5
1999	04/05/99	03/06/99	27	789.5
2000	22/05/00	23/06/00	31	775.5
2001	12/05/01	14/06/01	31	795.5
2002	11/05/02	13/06/02	26.5	760
2003	26/04/03	26/05/03	30	792.5

Figure II-6: Start and end days of the surveys. Julian day is the day of the year, where 120 corresponds to the 30th of April, 150 the 30th of May and 180 the 29th of June.
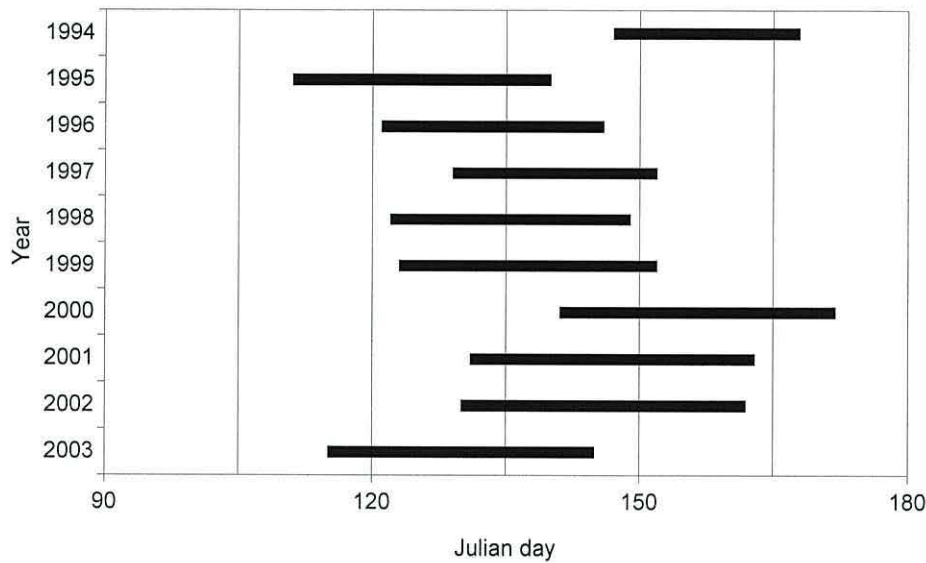
II-3. CHARACTERISTICS OF THE SAMPLED AREAS: THE MEDITERRANEAN COAST OF SPAIN

This section aims to introduce to the characteristics of the area, which in latter sections are related with *L. depurator* distribution.

The distribution and abundance of brachyuran crab populations depends on conditions which influence larval and adult survival. Those conditions differ widely between adults and larvae since adults are essentially benthic while the larvae are largely planktonic. Both abiotic (e.g. seawater temperature, chemistry and circulation, substratum type) and biotic (e.g. intra- and inter-specific competition for food or space and predation pressures) factors can set limits to or even regulate population abundance and species distribution. Adult crab populations cannot exist without recruitment from larvae but equally well supply of larvae is dependent on the health of the adult population. In high abundance species, such as *Liocarcinus depurator*'s recruitment has to be the primary determinant of population density.

Gorsky *et al.* (2002) estimated that about 10% of primary production reaches the sea floor in the North-Western Mediterranean. Variations in primary productivity will undoubtedly alter food availability for adult crabs, but is likely to produce more immediate effects on crab larvae which are more tightly coupled to water column dynamics. The main oceanographic currents not only determine patterns of primary productivity (e.g. the generation of upwelling regions) but they also determine direction and range of larval dispersal. Consideration of distribution and population characteristics of *L. depurator* would not be complete

without a description of the main oceanographic and biogeochemical features of the area surveyed.

The Mediterranean Sea can be considered as a reduced Ocean, formed by two main basins: western and eastern, which communicate through the strait of Sicily (see Figure II-7). The two basins have different oceanographic characteristics and water masses.

Figure II-7: Mediterranean Sea basins and separating sills (from diverse sources).
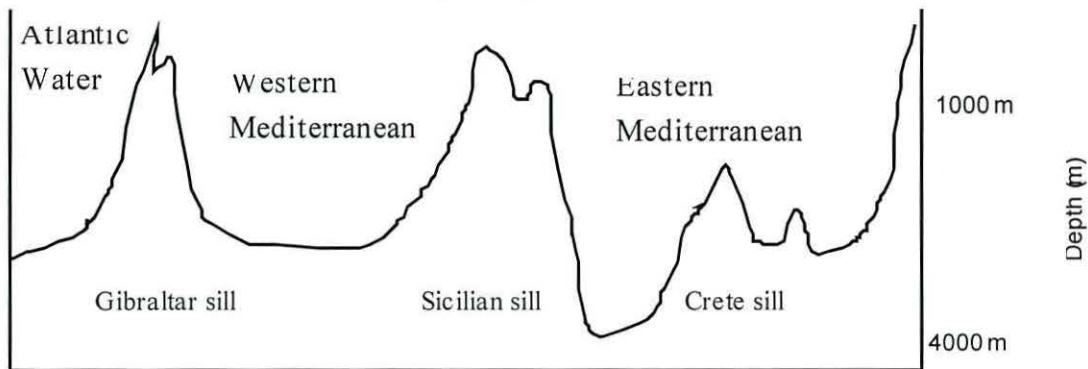
Large volumes of seawater are continuously exchanged between the Atlantic Ocean and the Mediterranean through the Strait of Gibraltar. Saltier, deep water flows out of the Mediterranean (mixture of Levantine Intermediate Water and western Mediterranean Deep water) fresher and lower nutrient concentration surface water enters from the Atlantic. Nutrient rich North Atlantic Central Water is periodically injected to the Mediterranean and enriches the inflowing Atlantic Surface Waters (Gomez et al., 2000). The mixing of these water masses near the Spanish coast can stimulate high primary productivity.

Eddies play a major role in the exchange of water masses along and across the western Mediterranean Sea by disrupting normal water mass flow, generating considerable extra mixing and changing the paths of the water masses (Salas, 2003, and ref. therein). Water mixing processes associated to eddy circulation may generate local increases in primary productivity. Furthermore, anticyclonic eddies have also been associated with the generation of coastal up-welling which usually induces increased phytoplankton biomass (Barton et al., 1998; Basterretxea et al., 2002; Kimura et al., 2000).

Figure II-8: SeaWIFS derived chlorophyll-a distribution in the Western Mediterranean. The image corresponds to 10 days averaged concentration values gathered during the month of May in the years 1998 to 2001.
http://www.me.sai.jrc.it/me-website/contents/shared_utilities/frames/archive_seawifs.htm

1998   1999

2000   2001
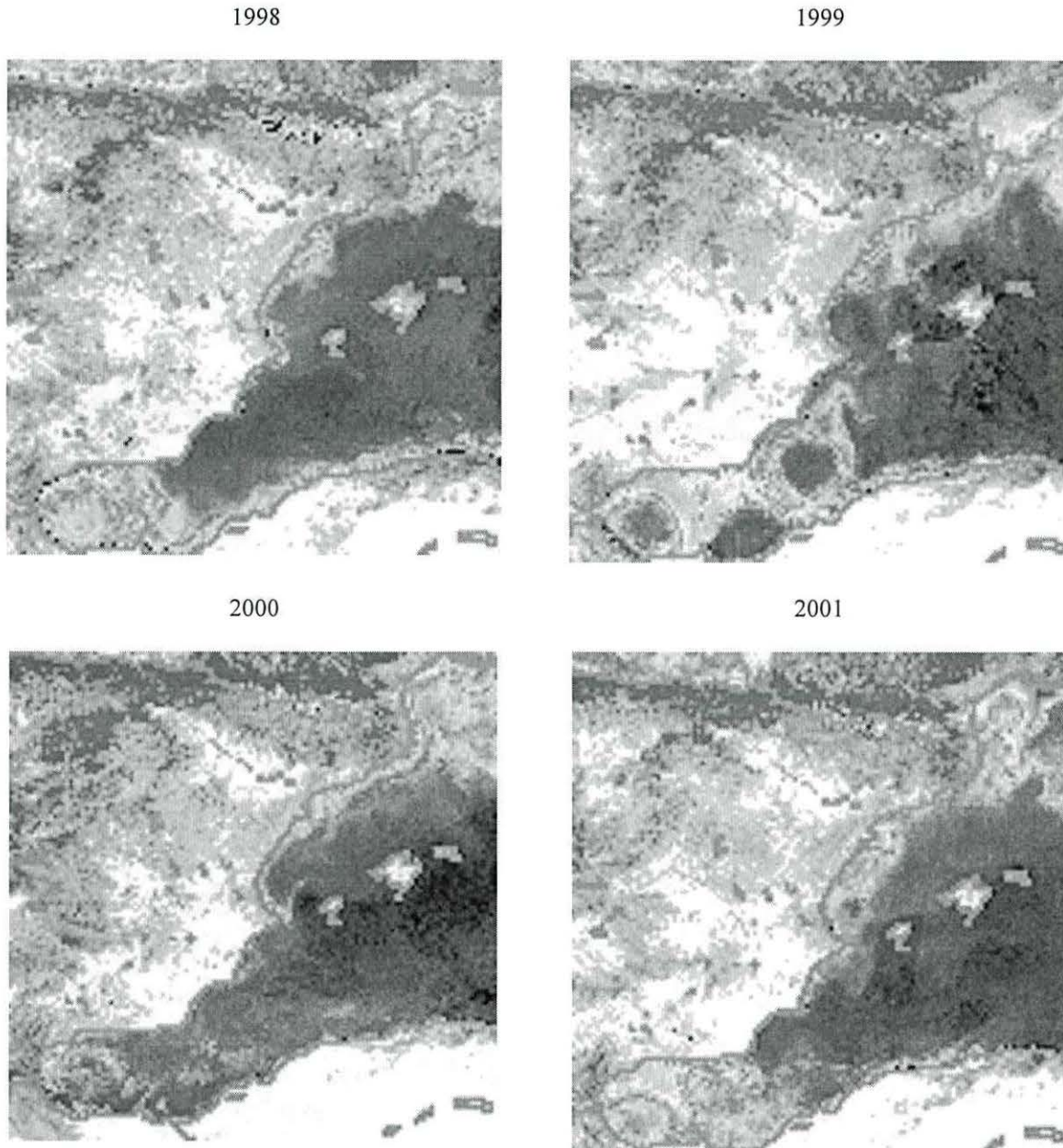
Legends:

Figure II-8: SeaWIFS derived chlorophyll-a distribution in the Western Mediterranean. The image corresponds to 10 days averaged concentration values gathered during the month of May in the years 1998 to 2001. http://www.me.sai.jrc.it/me-website/contents/shared_utilities/frames/archive_seawifs.htm

1998

1999

2000

2001

Legends:

0.01   0.1   1.   10.   64.
chlor-a mg/m3

0.0   0.2   0.4   0.6   0.9   1.0
SeaWIFS-VI / FAPAR
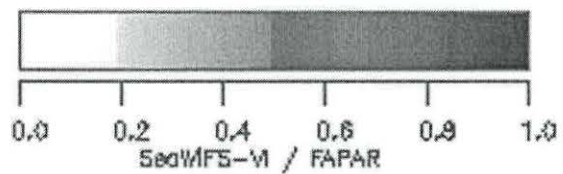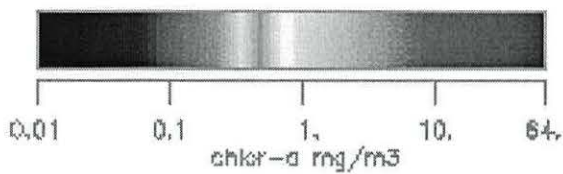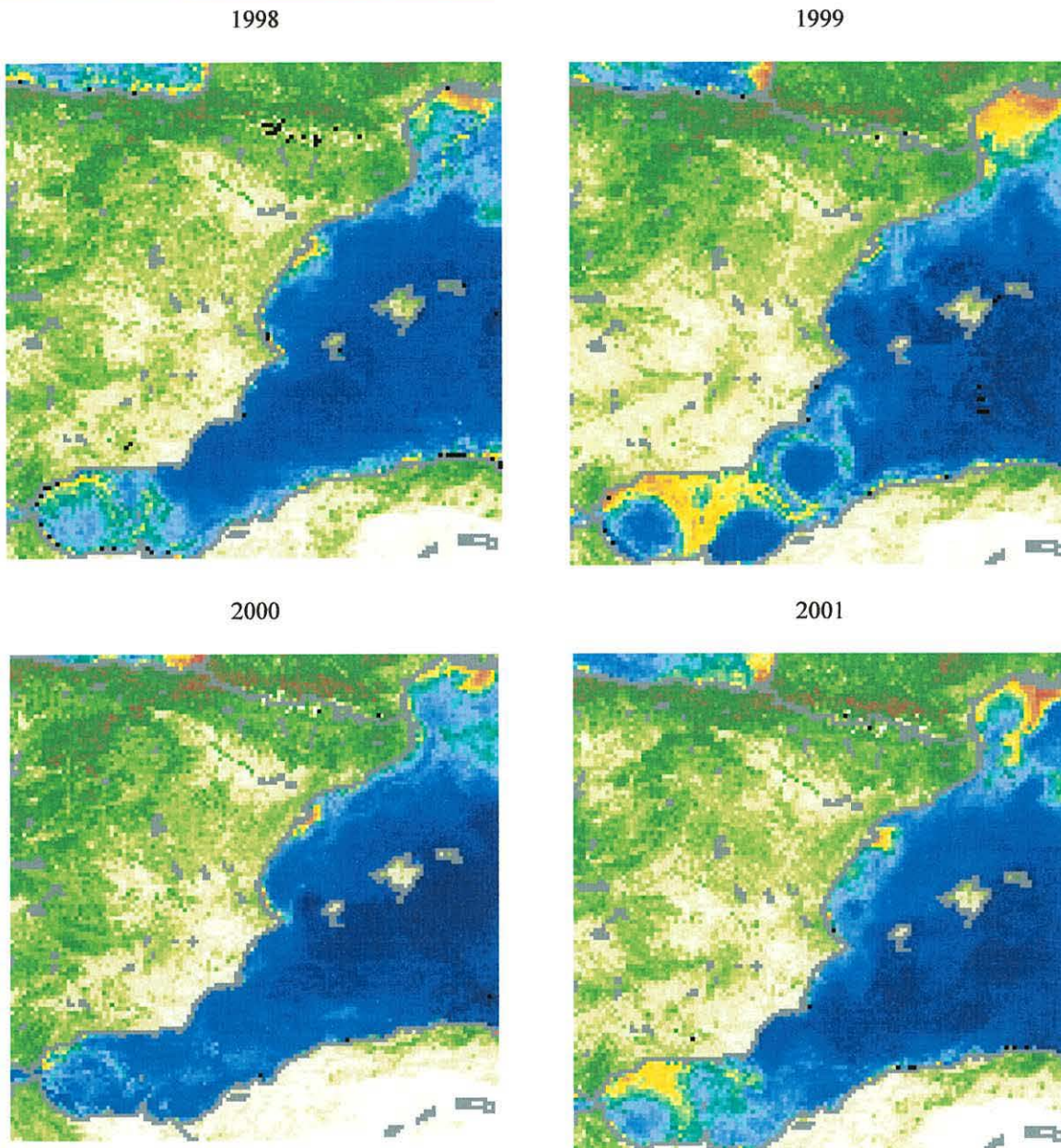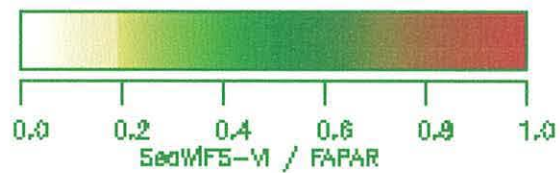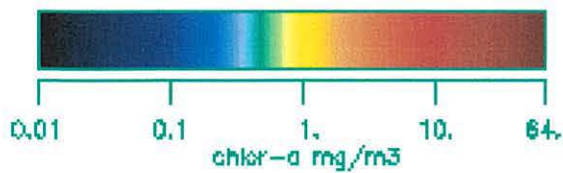
Figure II-9: Salinity measurements at 50 m depth, on all the Mediterranean Sea. Note the spread of the dark blue patch, which corresponds to the entrance of the Atlantic waters with lower salinity. Data from 1993 www.obs-mip.fr/.../rech/circu/ projects/circul_ang_medex.htm. Color bar indicate salinity levels. Map limits: longitude 5°W-15°E and latitude: 32°N-44°N.
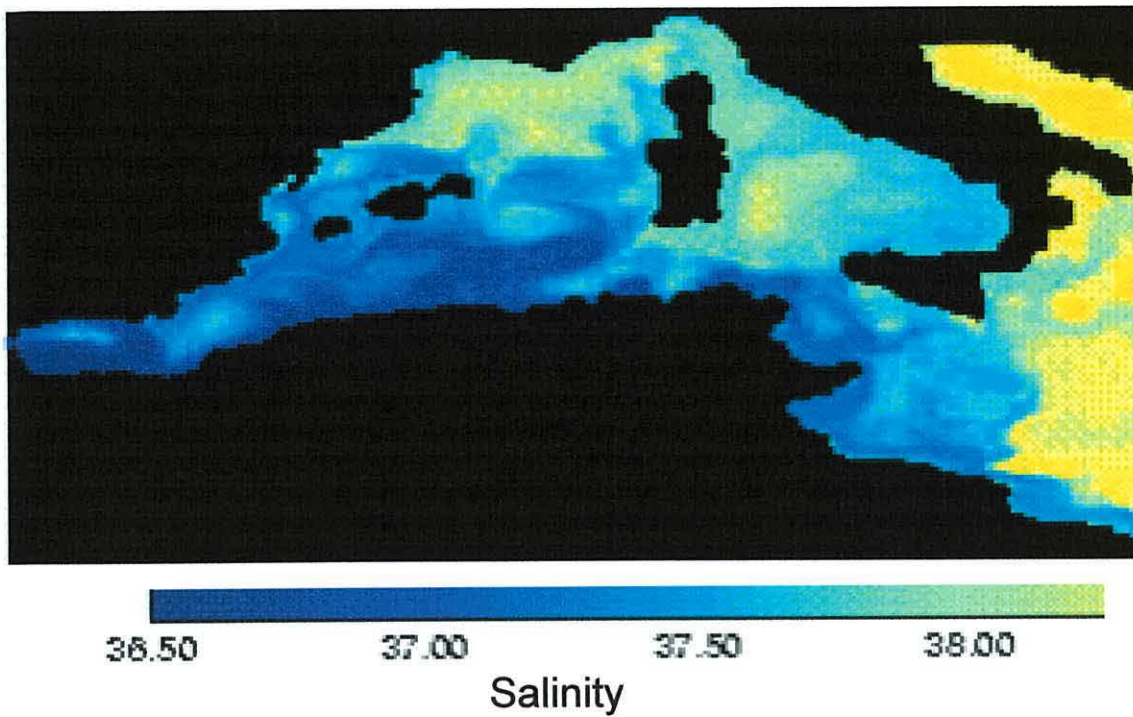
Figure II-10: Altimetry Alborán Sea eddy, summer 1997 (left picture). Seasonal variation of the sea eddies in the Gibraltar strait (Alborán Sea). Right color bar goes from –10 to 10 cm. (www-aviso.cls.fr/html/applications/ multi/med_time_uk.html).
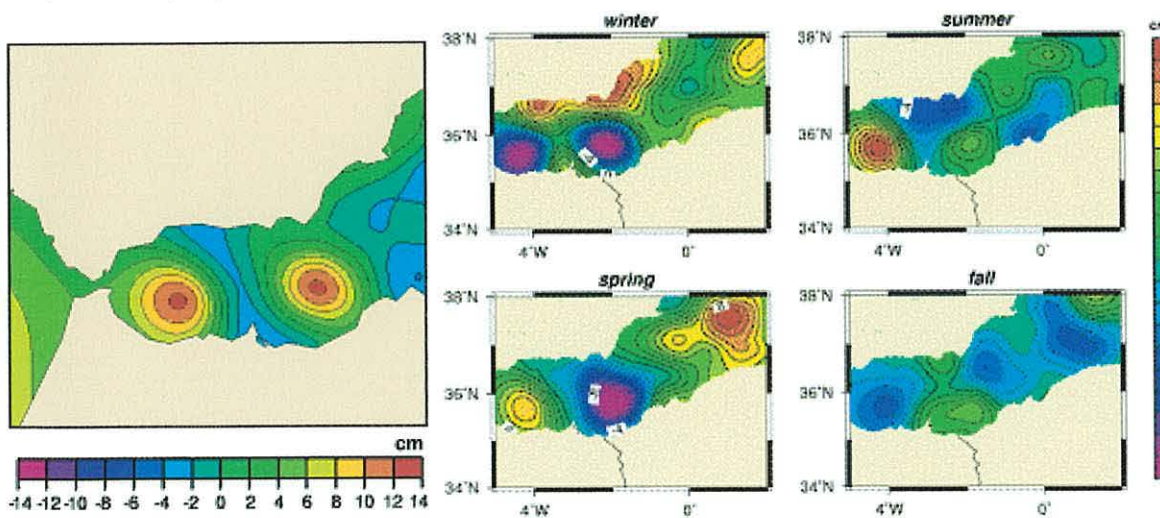
Figure II-11: Location of the areas, currents, eddies and upwelling zones described throughout the text. Legend: 1. Gibraltar sill; 2. Ibiza; 3. Mallorca; 4. Corsica; 5. Sardinia; 6. Sicily; a. West Alborán Eddy (anticyclonic); b. East Alborán Eddy (anticyclonic); c. Almeria-Orán front; d. Algerian current; e. Occasional Algerian eddies (open sea); f. Gulf of Lions eddy (cyclonic); g. local eddies (due to the canyons); h. Northern current (Liguro-Provençal). Grey shadow correspodns to upwelling areas.
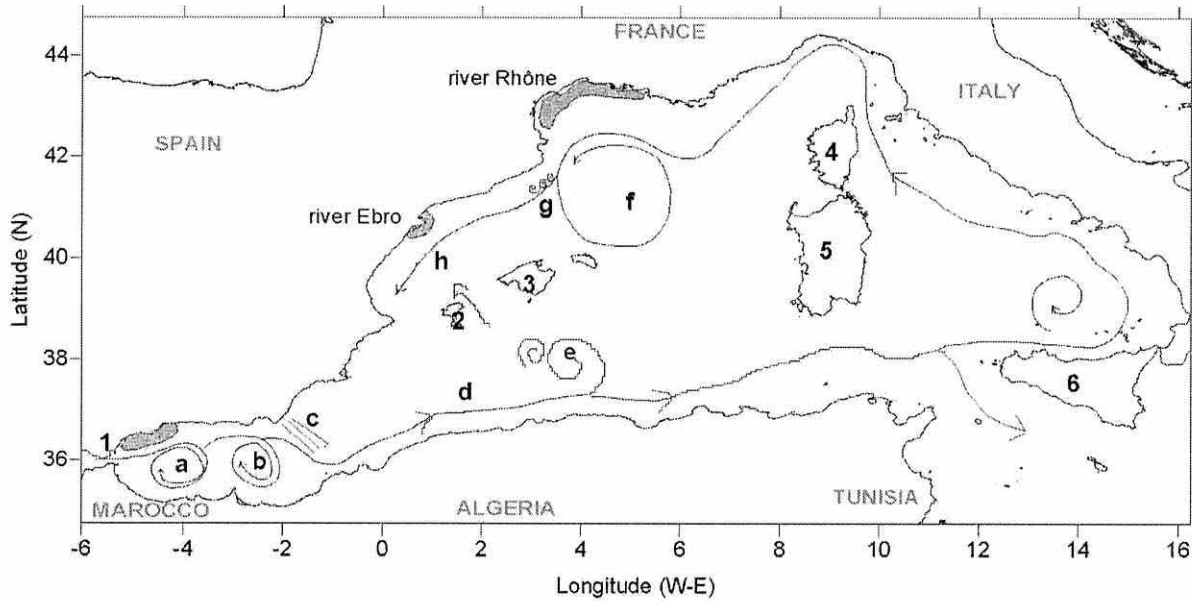
Figure II-12: Location of the main seas, in the Western Mediterranean.
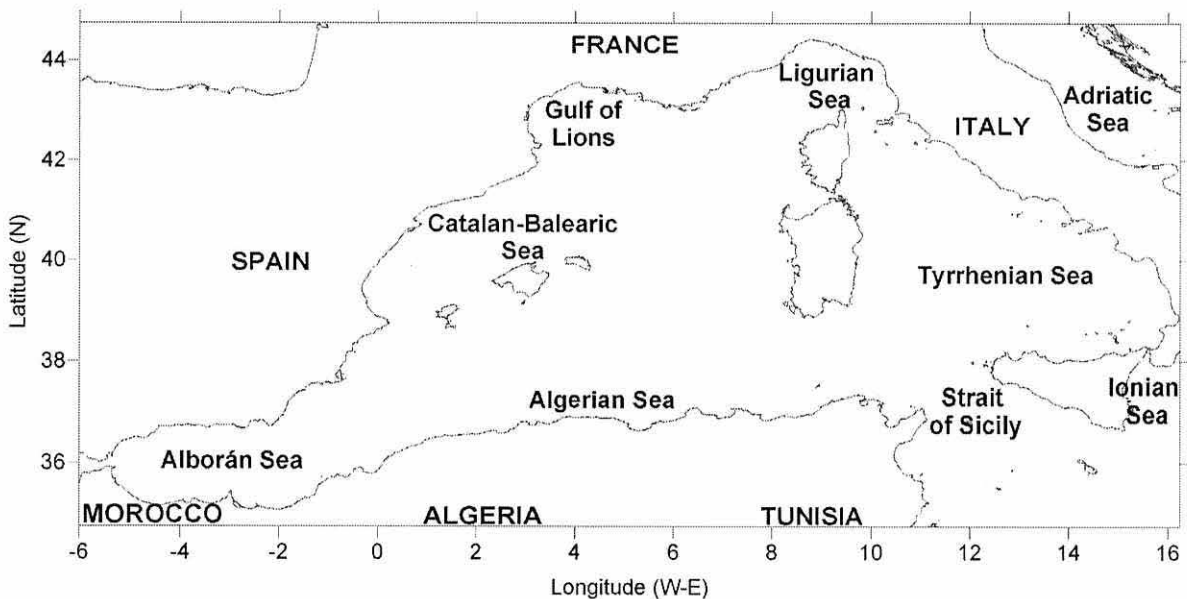
In the Alborán Sea, the Atlantic inflow generates quasi-permanent anticyclonic gyres in the west and more erratic circulation in the east (Millot, 1999)(Figure II-11). The eastern circulation is largely anticyclonic but occasionally it is driven cyclonic by strong easterly winds and may extend south-eastwards from Cape de Gata for several days (Millot, 1999). The incoming Atlantic water is then blocked at the Almería –Orán front and forced to move eastwards where it becomes the Algerian current, near the Algerian coast (Figure II-11 and Figure

II-12). The Algerian current may often generate local coastal eddies (which probably have no influence on the Spanish coast) but, occasionally, it generates open sea eddies which meander into the middle of the basin (Millot, 1999) (Figure II-11). These eddies leave the Algerian slope and, guided North by the slope contours in the Channel of Sardinia, usually reach the Balearic Islands (Millot, 1999) (Figure II-11).

The Northern Current in the Western Mediterranean, mainly composed of Modified Atlantic Water (Ligurian-Provençal current)(sensu Millot, 1999) originates in the Ligurian Sea and divides in two. The main one, streams westward towards the Channel of Ibiza (Figure II-11). Generally, in winter the current is narrow and flows near the coast, while in summer it is broad and flows further offshore (Gorsky *et al.*, 2002). The other flow branches off the main one in the Catalan-Balearic Sea and flows northwest, towards Corsica before being turned northeast, towards the French coast (Gulf of Lions). The presence of many submarine canyons in the northern part of Catalonia, creates several, small, regional eddies associated to the main southwestward flow. Additionally, the discards of the Rhone river (one of the most important in the Mediterranean) enrich the area with muddy and silt sediments.

Besides eddies and up-welling, the other major contributors to high coastal nutrient concentrations, are river discharges (Estrada *et al.*, 1985). Within the western Mediterranean, the Ebro and the Rhône's river deltas are the most productive areas of the coast (Estrada *et al.*, 1985). These rivers besides carry high concentrations of phosphate, nitrate and other nutrients but are also the main source of anthropogenic contamination. The river discharges also promote water mixing in which enhances the fertility of neighbouring areas (Estrada *et al.*, 1985) and carry considerable quantities of silt and clay particles which determine the nature of the bottom substratum in their vicinity.

The nature of the two main anticyclonic gyres (eddies) that are present in the Alborán basin differs throughout the year (Figure II-13, Figure II-10 and Figure II-8). The eastern Alborán gyre (Figure II-11) has been known to split, on occasions into as many as three eddies. During its eastward migration, inflowing Atlantic water is modified by mixing with the up-welled Levantine intermediate Water (LIW) forming Modified Atlantic Water (MAW). Satellite imagery shows that MAW meanders around the Alborán Sea until reaching Cape Gata, where it meets the westward flowing Mediterranean Surface Waters. The convergence causes the MAW to be deflected southeast towards Orán (Algeria) along the eastern edge of the Eastern Alborán Gyre, forming the well-defined Almeria-Orán front (Fielding *et al.*, 2001, and references therein).

The Alborán Sea receives nutrients through eddy-induced upwelling in the periphery of the gyre path (Garcia-Gorriz & Carr, 2001)(Figure II-8, Figure II-10 and Figure II-13). The

rate of circulation determines the nutrient supply and hence the phytoplankton biomass in the upper layer, from late spring and through summer to early autumn, i.e. later than the spring phytoplankton bloom. Baldacci *et al*l. (2001) studied the formation of the upwelling systems in the Alborán Sea during 1997-1998, identifying two main areas (Figure II-13). The western gyre forms an upwelling region between 5.5°W and 4.5°W while the eastern gyre forms a larger upwelling region between 4.5°W and 2°W (area B, Figure II-13) (Baldacci *et al.*, 2001). Upwelling dynamics in area A are controlled by the influence of both coastal and eddy induced upwelling while in area B only eddy induced upwelling plays a relevant role.

Figure II-13: Main currents and gyres generated in the Alborán Sea and respective upwelling areas described in the text (from Baldacci *et al.*, 2001).

a)

b)
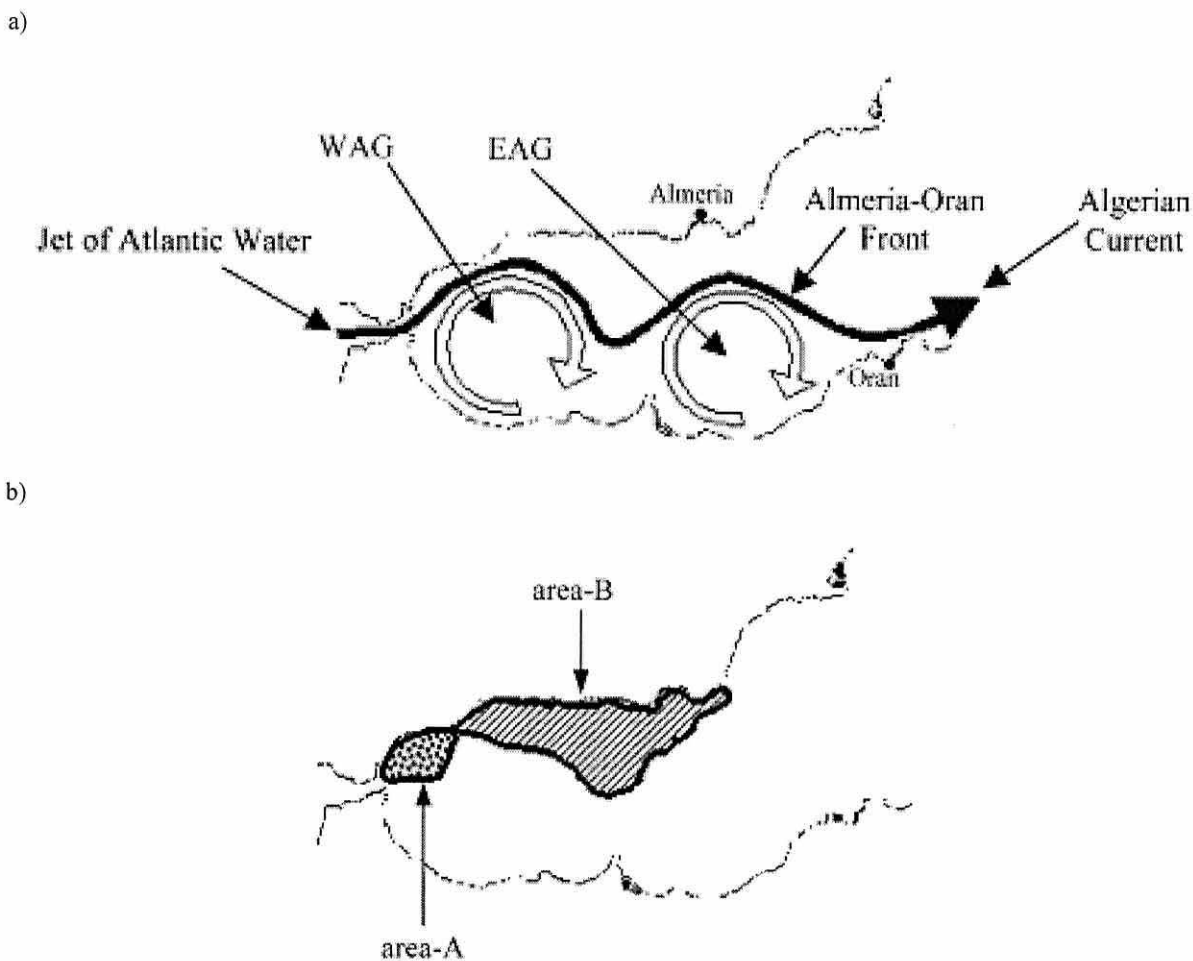
The Gulf of Vera, located between Cape Gata and Cartagena, is much less influenced by the lower salinity MAW since, around the region of Almeria, the Atlantic jet veers off the coast and flows southeastwards along the Almeria-Orán front. Abelló *et al.* (2002) found that the crustacean community of the Alborán Sea is biogeographically quite distinct from that in the rest of the Western Mediterranean. However, the Alborán Sea and the Gulf of Vera share

a number of geological and oceanographic characteristics, most notably the narrowness of the continental shelf that controls the limited distribution of shelf species in that area. Abelló, (2002) also suggests that the stability of the Almería-Orán front contributed to the differentiation of the crustacean community characterised by 'Atlantic' species south-west Cape Palos and a community characterised by more 'Mediterranean' species north-east Cape Palos.

The continental shelf broadens in the vicinity of Alicante and Ibiza where inflowing Atlantic and outflowing Mediterranean waters meet and the Atlantic current is driven south near the Ibiza sill (Figure II-7 and Figure II-11). Up-welling has been observed, occasionally, in the area of Cape la Nao and south between Alicante and Valencia. This upwelling events produce patches of high productivity and are probably associated with the formation of coastal anticyclonic eddies generated by the Algerian current instability (Figure II-14 and Figure II-11)(Salas, 2003).

Figure II-14: Eddie AE98-1 SST image of June 10th 1998. (from Salas, 2003)
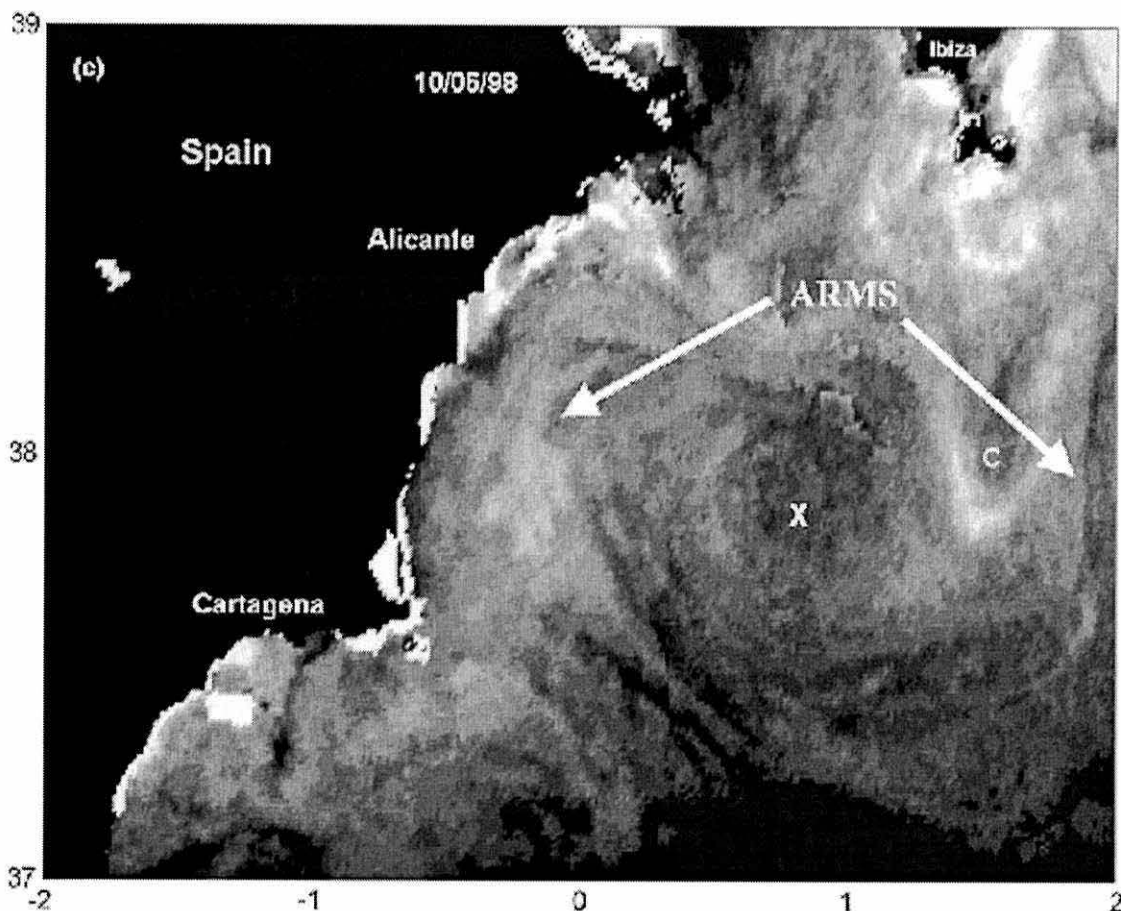
Despite the fact that the general circulation patterns are known there are few studies on the detailed oceanographic characteristics of the coast of Valencia. Onshore at Valencia, large land extensions are devoted to intensive agriculture (i.e. oranges), which implies the use of

large amounts of pesticides and other anthropogenic residuals that are delivered through various modes to the sea.

The Balearic Sea (Figure II-12) is a transitional area in the Western Mediterranean where surface (0-100 m) water masses of southern and northern origins meet. Cool, more saline, northern waters flowing from the Gulf of Lions formed by the presence of a cyclonic gyre that brings the deeper waters into the surface (Figure II-11 and Figure II-12), encounter waters of Atlantic origin flowing northward from the southern Algerian basin. The Balearic Isles (Figure II-12) ridge represents a complex topographical barrier where water exchange takes place in two channels: the Ibiza Channel, between Ibiza and the Spanish peninsula, and the Mallorca Channel between Ibiza and Mallorca. Pinot *et al.* (2002) have recently shown that the Mallorca Channel carries mostly southern water in its northward spread. Northward flow along the Mallorca Channel can be reversed during winter and spring as more, cool, southward-flowing waters of northern origin reach the channel.

Around the Ebro Delta and the Columbretes islands the continental shelf reaches its maximum width (up to 70 km) due to the progradational nature of the Ebro Delta margin. This area is highly productive due to the combined effect of the northern current that hugs the continental slope (Millot, 1999) and the runoff of the Ebro River (Figure II-12)).

In the central-north Catalonian area the continental shelf becomes narrow again, and its whole margin is indented by submarine canyons. These canyons act as a barrier that deflects the large scale south-ward flow, promoting the formation of local small scale eddies in this area (Figure II-11 and Figure II-12).

In the northern part of the area, the Rhône river discharge has a considerable indirect influence on nutrient and sediment loading as well as water mixing processes (Figure II-12).

III. Geographical, bathymetric, and inter-annual variability in distribution of *Liocarcinus depurator* (Brachyura: Portunidae) along a western Mediterranean coast

III-1. ABSTRACT

The occurrence and density of *Liocarcinus depurator* along the western Mediterranean coast (from Gibraltar to Cape de Creus) was measured at depths between 25 and 800 m. Bottom trawl surveys were carried out, from 1994 to 2003. The area was divided into 8 geographic sectors and 8 depth intervals. Percentage occurrence of *L. depurator* was calculated as the number of hauls where the crab appears, in relation to the number of hauls performed. Highest crab occurrences and densities were found at 51-100 m depth (80%, 985 crabs.km^{-2} on average, 342 hauls) with a second, smaller peak of occurrences at 301-400 m (66%, 33 crabs.km^{-2} on average, 80 hauls). Densities were greater but occurrences lower at 201-300 m depth (57%, 130 crabs.km^{-2} on average, 74 hauls). Deeper than 500 m, crab occurrences (hence densities) dropped sharply and were always below 10%. Maximum crab occurrences and densities were observed in the area of Valencia (86%, 1187 crabs.km^{-2} on average, 93 hauls) and West Alborán (83%, 974 crabs.km^{-2} on average, 112 hauls) followed by the Ebro Delta (75%, 502 crabs.km^{-2} on average, 188 hauls). Alicante area had large numbers of occurrences in samples but relatively lower densities (74%, 294 crabs.km^{-2} on average, 162 hauls), whereas north Catalonia had lower crab occurrence (53%), but relatively high densities (317 crabs.km^{-2} on average, 185 hauls). Otherwise, the pattern of occurrences closely accompanied that of the densities. Densities decreased from 1994 to 2003, at a rate of 8 and 4% in shallower and deeper than 150 m, respectively. During 2003, the lowest number of crabs were caught since the beginning of the survey.

III-2. INTRODUCTION

Liocarcinus depurator is a continental shelf portunid crab whose bathymetric distribution also extends to the upper shelf slope (Abelló *et al.*, 2002; Abelló *et al.*, 1988; González-Gurriarán *et al.*, 1993; Mori & Zunino, 1987; Ungaro *et al.*, 1999b). It is a temperate-water species ranging in distribution from the coasts of the western Sahara, west Africa to Norway, including the Mediterranean Sea (d'Udekem d'Acoz, 1999). *L. depurator* is one of the most abundant members of the commercially exploited soft-bottoms, shelf communities (Abelló *et al.*,

2002; Abelló *et al.*, 1988; González-Gurriarán & Olaso, 1987; Ungaro *et al.*, 1999b). It is both a major predator and prey item for several epibenthic and benthic species, including commercial species (Abelló & Cartes, 1987; Cartes *et al.*, 2002; Demestre *et al.*, 2000; Freire, 1996; Hall *et al.*, 1990a; Mori & Manconi, 1989; Olaso, 1989). Given its widespread occurrence, the study of the variability in its distribution patterns, geographic, bathymetric and temporal, should provide insight to the factors affecting its populations dynamics and hence the impact of *L. depurator* within its community.

Fishery-independent demersal trawl surveys can provide a wide range of information, not only on target species, but also on the key members of the benthic communities. Trawl time series surveys, even if from short periods, are rare but can supply far more information on communities than isolated random surveys which lack the continuity to allow temporal interpretation. The aim of the present work is to compare the occurrence and density of *L. depurator* through a 10 year series of standardised trawl surveys (MEDITS project: Bertrand *et al.*, 2000; Bertrand *et al.*, 2002) along the Mediterranean coast of the Iberian Peninsula.

III-3.   MATERIALS AND METHODS

III- 3.1. Survey details

The study area (described in detail in section II) encompassed the Mediterranean coast of Spain, from Gibraltar to Cape Creus (Figure II-5). A bottom trawl survey performed took place annually from 1994 to 2003 (Bertrand *et al.*, 2002). Survey stations were chosen by stratified random sampling with strata delineated by depth and geography. The sampling strategy produced a compromise between statistical adequacy and the needs of geostatistical analysis (Bertrand *et al.*, 2002).

The depth intervals employed were those used by Abelló *et al.* (2002): 50 m intervals down to 200 m depth and 100 m intervals on the shelf slope. Although Bertrand *et al.* (2002) defined only three broad geographical sectors, the high sampling density allowed smaller areas to be defined on the basis of different geomorphology and hydrography (Abelló *et al.*, 2002). Thus, Abelló *et al.* (2002), divided the coast into eight regions which also apply to the current study (see Figure II-5): (1) Western Alborán Sea (WALB), from Gibraltar to Nerja; (2) Eastern Alborán Sea, from Nerja to Cape Gata; (3) Vera Gulf (VERA), from Cape Gata to Cape Palos; (4) Alicante (ALIC), from Cape Palos to Cape La Nao; (5) Ibiza island (IBIZ); (6) Valencia (VALE), from Cape La Nao to Castellón; (7) Ebro Delta region (DELT), from Castelló to Tarragona and (8) North Catalonian (NCAT), from Tarragona to Cape Creus.

The sampling gear throughout (GOC 73 Fiorentini *et al.*, 1999) was designed for scientific sampling rather than commercial fishing (see section II). Hauls taken at depths shallower than 200 m lasted 30 minutes whereas the deeper trawls lasted 60 minutes. All *Liocarcinus depurator* individuals were counted, weighed and linear dimensions measured immediately after capture. Density was then standardised to swept area (number.km^{-2}).

From 1994 to 2003, a total of 1098 hauls were performed in 45331 km^2, off the Spanish Mediterranean coast of Spain. Figure III-1 shows the distribution of the 77 to 135 hauls taken each year. Only the Ibiza and Alborán Island (in the south of East Alborán) areas were not sampled every year and thus were excluded from the analysis (Figure III-1). Furthermore, the northern part of the NCAT sector (North Catalonia) was not sampled in 1998. Whenever possible, the same stations were sampled each year. The number of hauls in each sector varied with the width of the shelf and shelf-slope. Thus, the Gulf of Vera (VERA) was sampled less intensively owing to the steepness of the continental shelf-slope whereas the Ebro Delta (DELT) was sampled more intensively because of its wide continental shelf. During 1994, the initial year of the project, sampling was less exhaustive as protocols were being established.

Figure II-6 shows that sampling took place from the end of April though to June, with small differences in timing from year to year. Thus surveys in 1994 and 2000, ended on the 19th and 23rd June (respectively) and those in 1995 and 2003, ended on 21st and 26th of May (respectively). The earliest start and the latest finish dates for the surveys were 22/4 (1995) to 23/6 (2000) a period of two months (Table II-3).

Table III-1: The number of hauls performed in each geographic area and depth interval (m). See Figure II-3 for the abreviations of the sectors.

Depth	WALB	EALB	VERA	ALIC	IBIZ	VALE	DELT	NCAT	Total
25-50	13	9	3	20		8	33	17	103
51-100	33	22	11	55		50	118	53	342
101-150	13	8	5	23	3	23	29	50	154
151-200	9	5	8	17		3	4	9	55
201-300	13	9	13	13	8	2	1	15	74
301-400	23	12	5	12	2	7	1	18	80
401-500	8	12	5	22	8		2	23	80
501-600	20	17	7	24	9	1		23	101
601-700	27	15	2	2	6			18	70
701-800	18	3	6		2	8		2	39
Total	177	112	65	188	38	102	188	228	1098

Confidence intervals of the medians were estimated with Wilcoxon test (corrected for tied values). Confidence intervals of the percentages were calculated as $p\pm1.96*\sqrt{p*q/n}$, where p is the percentage and n the number of samples.

III-4. RESULTS

III-5. OCCURRENCES

Figure III-1 shows that *Liocarcinus depurator* occurred throughout the surveyed area. In certain regions, Ebro Delta for example, crabs are consistently found each year. In other areas, the northern part of North Catalonia for example, *L. depurator* occurrences decreased markedly towards the end of the sampling period. Table III-2 shows the percentage occurrence of *L. depurator* in each depth interval and geographic location.

L. depurator occurred at all sampled depths, although its greatest percentage occurrence (~80%) was at 51-100 m. Between 151 and 400 m crabs appeared in 55-66% of all hauls and the percentage occurrence dropped sharply after 500 m (7-8% of all hauls). Trawls from more than 500 m were therefore excluded from further analysis. Figure III-2 shows the percentage occurrence ($\pm$ CI$_{95\%}$) of *L. depurator* with depth across all regions and sampled years. The occurrence shows a very consistent percentage between 55-66% with considerable overlap in CI$_{95\%}$ over the depth range of 25-350 m. The small CI at 51-100 m results from the intensive sampling at those depths (342 out of 1098 tows)(Table III-1). The distribution with depth is distinctly bimodal with one mode at 51-100 m and a smaller one at 301-400 m. Occurrence then drops sharply over the next 200 m with only 16 out of 210 trawls yielding *L. depurator* below 500 m.

Table III-2: Percentage occurrence of *L. depurator* in each geographic area and depth interval, throughout the Mediterranean coast of Spain. 'Total (<500 m)' indicates the percentage occurrence for depths shallower than 500 m. See Figure II-3 for the abreviations of the sectors.

Depth/sector	WALB	EALB	VERA	ALIC	IBIZ	VALE	DELT	NCAT	Total
25-50	76.9	0	33.3	55.0		37.5	66.7	64.7	56.3
51-100	90.9	31.8	63.6	81.8		92.0	83.9	71.7	79.5
101-150	84.6	37.5	40.0	91.3	0	95.7	51.7	48.0	63.6
151-200	100	60.0	50.0	64.7		33.3	0	22.2	54.5
201-300	100	66.7	23.1	76.9	0	100	100	46.7	56.8
301-400	69.6	58.3	0	100	50.0	85.7	100	55.6	66.3
401-500	50.0	50.0	0	40.9	12.5		100	30.4	36.3
501-600	5.0	5.9	0	4.2	0	0		21.7	7.9
601-700	14.8	0	0	0	0			5.6	7.1
701-800	5.6	0	0		0	12.5		5.0	7.7
Total	55.9	29.5	26.2	63.8	5.3	79.4	74.5	46.5	54.5
Total (<500 m)	83.0	41.6	34.0	73.5	9.5	86.0	74.5	53.5	65.5

Figure III-1: The presence (●) and absence (o) of *Liocarcinus depurator* throughout the study area from 1994 to 2003. Longitude scale refers to the first map only. Contour lines represent 200 and 1000 m depth. See Figure II-3 for the abreviations of the sectors. Longitude scale refers to the first left bottom graph, the remaining graphs are repetitions with the same scale.
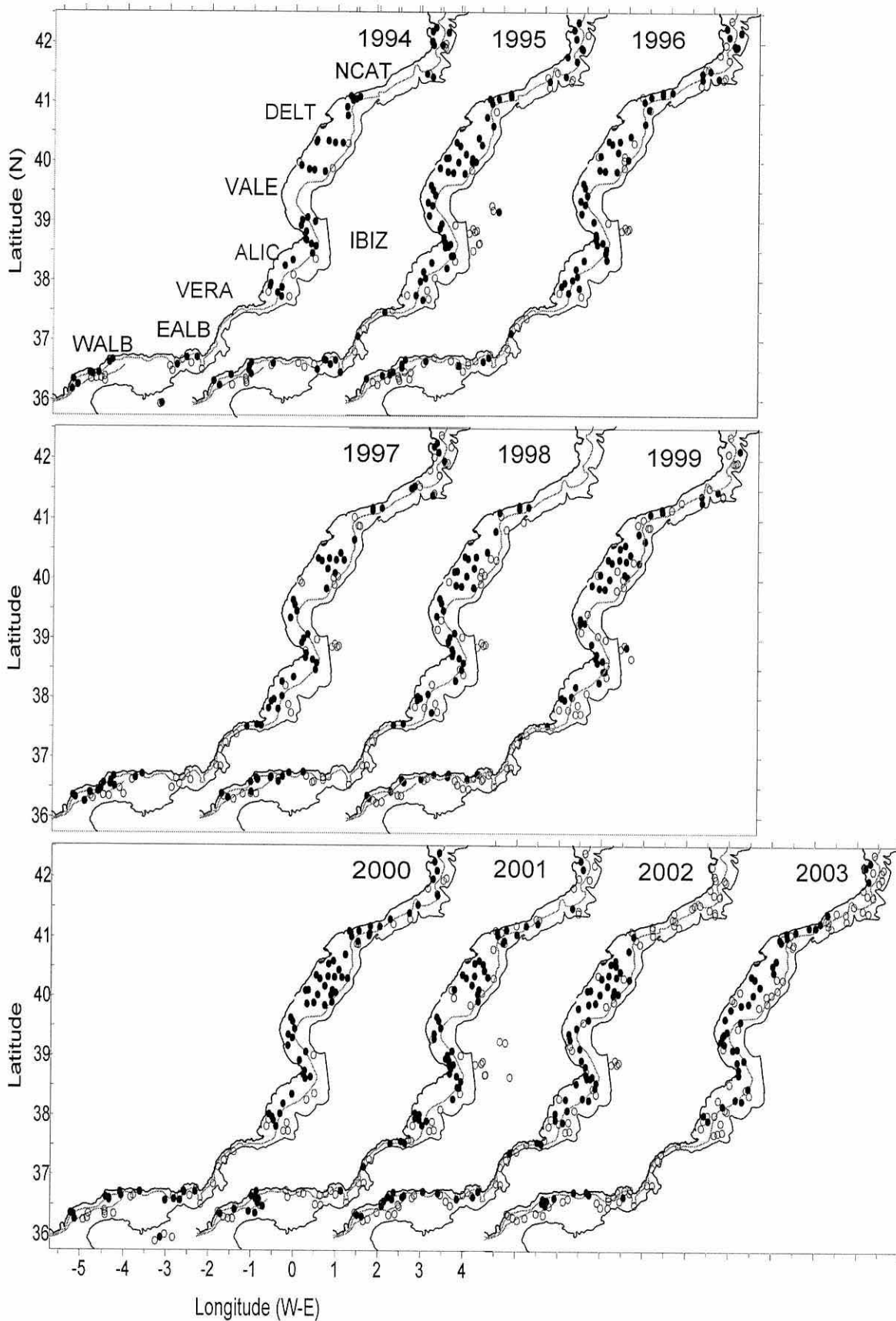
Figure III-2: Percentage occurrence of *L. depurator* (± CI$_{95\%}$) with depth along the Mediterranean coast of Spain from 1994 to 2003.
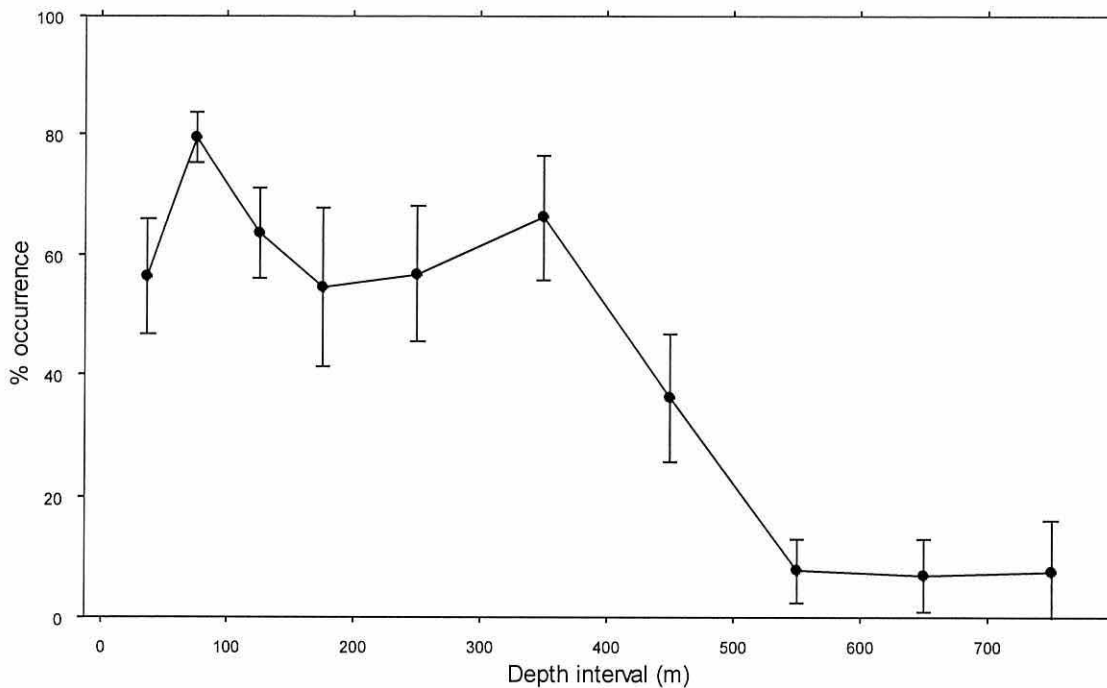
Geographical variability

Table III-2 indicates that Valencia, West Alborán, the Ebro Delta and Alicante showed the highest percentage occurrence of *L. depurator* averaging between 74-86% over depths <500 m. At Vera and East Alborán occurrences average 34-42% and 54% in North Catalonia. In the Ibiza area, occurrences, even in the shallower waters, were less than 10%. Ibiza was therefore excluded from further analysis.

Interannual variability

Table III-3 summarises the occurrences of *L depurator* along the Mediterranean coast of Spain from 1994 to 2003, There has been a general increase in the number of hauls taken over the ten years from a low 77 in 1994 to a high 135 in 2003. Figure III-2 shows the percentage occurrence (±CI$_{95\%}$) at depths shallower than 500 m, averaged across the geographic areas. There is a clear decreasing trend in occurrence (Kendal's tau= -0.73, T = 6, p = 0.002), showing an average decrease of 3.5% per year. Superimposed on the general trend are two peaks in occurrence followed by a decreasing trend in succeeding years. These are evident from 1995 to 1999 and 2000 to 2003. The average rate of decrease during these two periods was ~8% per year, more than double that of the general trend. During 2003, the year with the highest sampling effort, *L. depurator* occurrence reached its lowest annual level (51%).

Table III-3: The percentage occurrence of *L. depurator* in waters less than 500 m deep along the coast of Spain from 1994 to 2003.

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Total hauls	77	106	105	100	92	116	111	122	134	135
Total hauls (<500 m)	62	84	81	81	74	92	92	99	112	111
Total hauls with crab	53	72	62	55	50	54	73	64	59	56
Hauls with crab at <500 m	51	71	58	54	48	52	73	60	59	56
% Hauls with crab at <500	82.3	84.5	71.6	66.7	64.9	56.5	79.3	60.6	52.7	50.5

Figure III-3: The percentage of hauls in which *L. depurator* occurred ($\pm$ CI$_{95\%}$) at depths shallower than 500 m, along the Mediterranean coast of Spain, from 1994 to 2003.
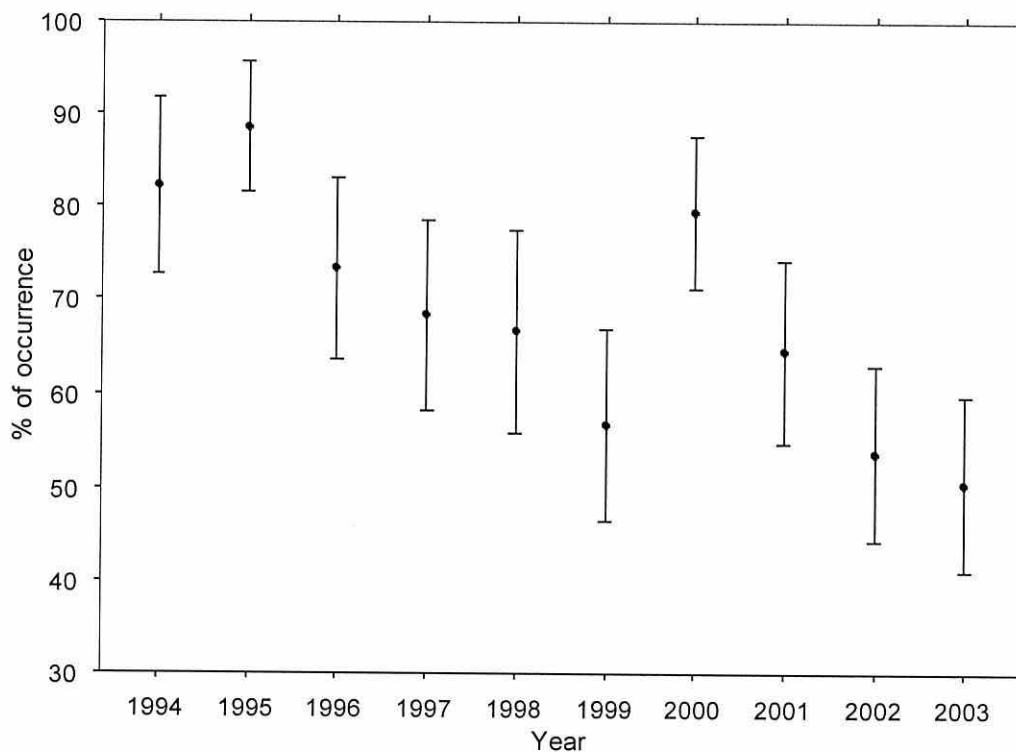
Figure III-4 shows that there was no consistent pattern of occurrence change over the 10 years of the survey within any depth range. Significant correlations were observed at 51-100 m, 201-300 m and 301-400 m. However given the overlap in CI$_{95\%}$, even those significant correlations show inconsistent annual patterns. For example the significant correlation (Kendal's tau= -0.49, z = -1.99, p = 0.046) for 301-400 m derives from a constant percentage of 80-85% from 1994-1998 and another of about 40-60% between 1999 and 2003 (Figure III-4). Furthermore the more linear looking trend for 51-100 m, shows a constant 80% occurrence from 1996 to 2001 with 90% in 1994-1995 and 70% in 2002-2003, so hardly a good fit to a decreasing linear relationship. The depth is compounded with the geographic location, which exhibits almost as much variability making it difficult to interpret interaction effects in the percentage occurrence relationship to time. All correlation coefficients were, however, nega-

tive resulting in a significant downward trend in percentage occurrence overall depths and areas from 1994 to 2003.

Figure III-4: Annual variation of the percentage occurrence (± CI$_{95\%}$) of *Liocarcinus depurator* grouped into depth intervals (m). The value of Kendal's tau, is indicated in the bottom left corner of each figure, followed by an * when significant. Lines fitted to significant relationship by least squares regression are merely indicative of the trend.
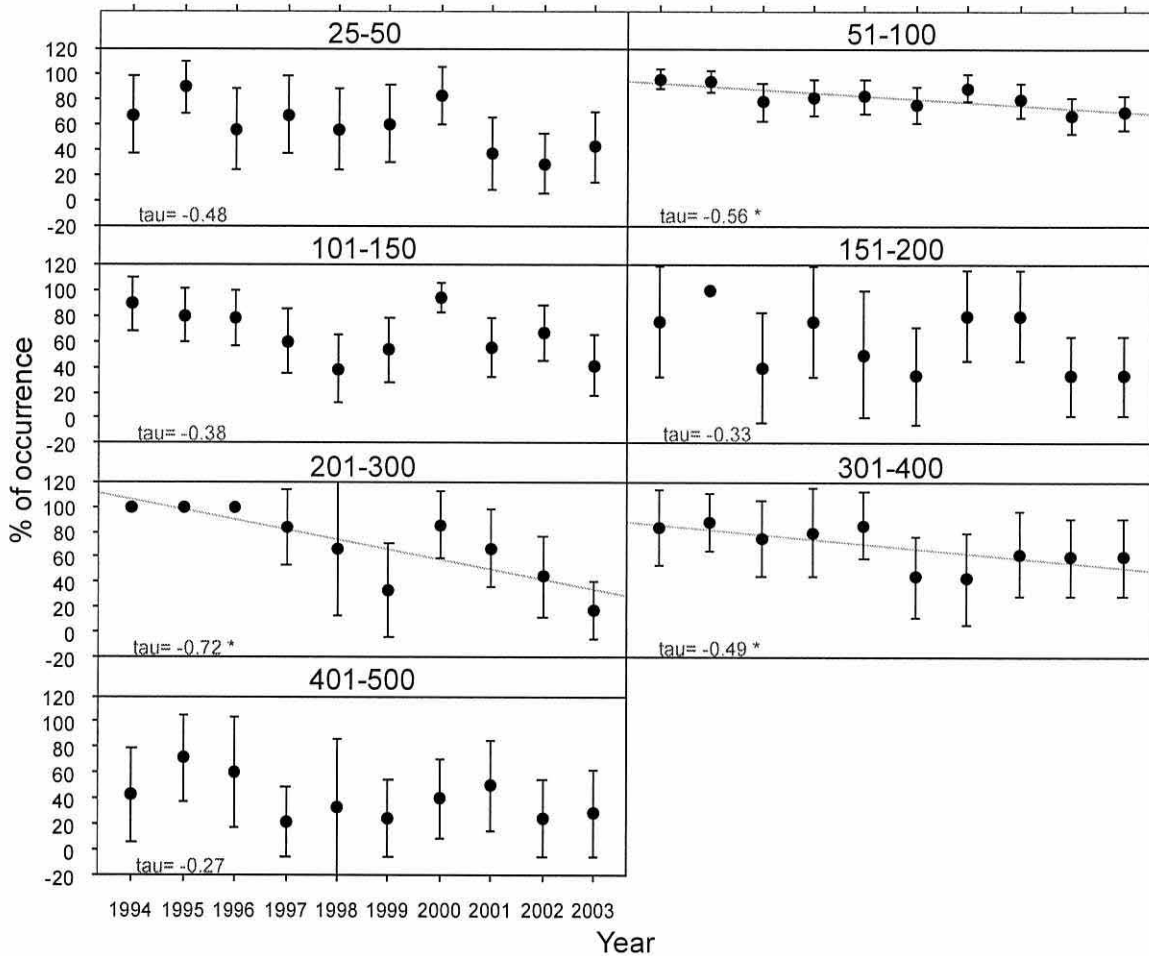
Figure III-5 shows the percentage occurrence (±CI$_{95\%}$) for depths shallower than 500 m in each geographic area of the Spanish coast. As with depth, no consistent patterns are clear annually except that all correlation coefficients were negative. Percentage occurrences at North Catalonia and Alicante showed significant correlations with time, but in neither case was there a good fit to a linear model (see Figure III-5). Again, interactive effects with depth undoubtedly cloud any consistent pattern but the general trend with year, across depths, is reflected in all correlation coefficients being negative even if not significant.

Figure III-5: Annual and geographic variation of the percentage occurrence (± CI$_{95\%}$) of *Liocarcinus depurator*. The value of Kendal's tau, is indicated in the bottom left corner of each figure, followed by an * when significant. Lines fitted to significant relationships by least squares regression are merely indicative of the trend. See Figure II-3 for the abreviations of the sectors.
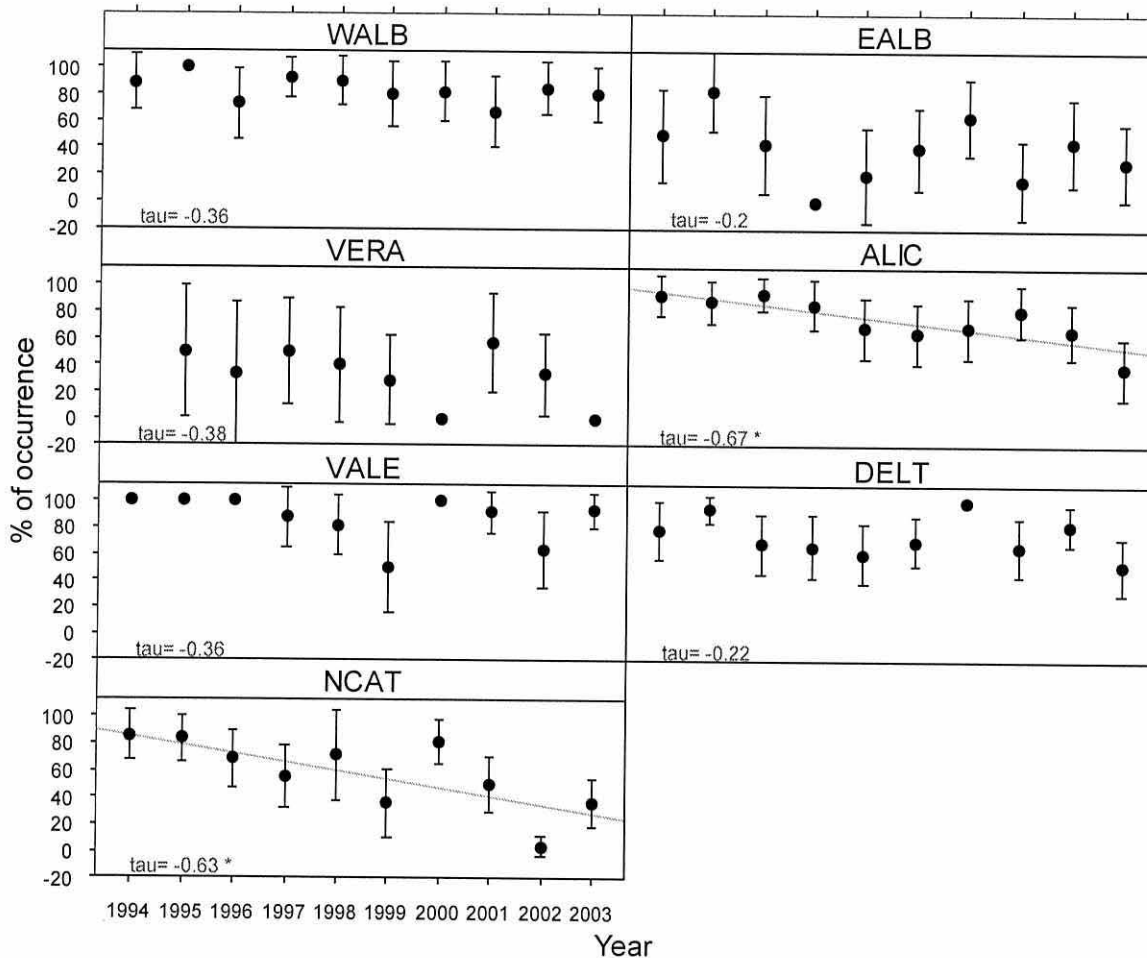
III- 5.1. Density

Table III-4 shows mean densities of *L. depurator* averaged over the whole sample area and all 10 years. The highest densities occurred in the 51-100 m depth range for all regions except East Alborán, where densities were similar across the 51-150 m range. Maximum average densities were observed at West Alborán (~2700 crabs.km^{-2}) and Valencia (~1900 crabs.km^{-2}) representing an area of 370-530 m^{-2} per crab. The frequency distribution of crab densities was heavily skewed (skeweness raging from 2.35 in 1995 to 7.08 in 1999 data), thus for improved visualisation, densities were log$_{10}$ transformed. In general, the trend in densities with depth resembled that for occurrence (see Figure III-6) with crab densities generally highest in shallower water but the second mode shown for occurrences in Figure III-2 is not as clear with density. The depth range from 101-300 m shows very similar, intermediate densities on aver-

age (120-200 crabs.km^{-2}). Below 500 m, densities decrease steadily to very low densities below 500 m (see Figure III-6).

Table III-4: Mean density (number.km^{-2}) of *L. depurator* in each geographic area and depth interval, throughout the Mediterranean coast of Spain. See Figure II-3 for the abreviations of the sectors.

Depth	WALB	EALB	VERA	ALIC	IBIZ	VALE	DELT	NCAT	Total
25-50	633	0	44	88		24	553	195	310
51-100	2677	96	265	543		1881	620	873	985
101-150	195	102	21	327	0	600	91	130	220
151-200	223	17	108	180		7	0	39	116
201-300	307	206	14	139	0	602	29	35	130
301-400	135	41	0	256	6	155	93	53	110
401-500	106	25	0	23	2		105	35	33
All depths <500	974	73	84	294	2	1187	502	317	484

Figure III-6: The variation in *L. depurator* median density (log$_{10}$(number · km^2+1)) (± CI$_{95\%}$) with depth along the Mediterranean coast of Spain from 1994 to 2003.
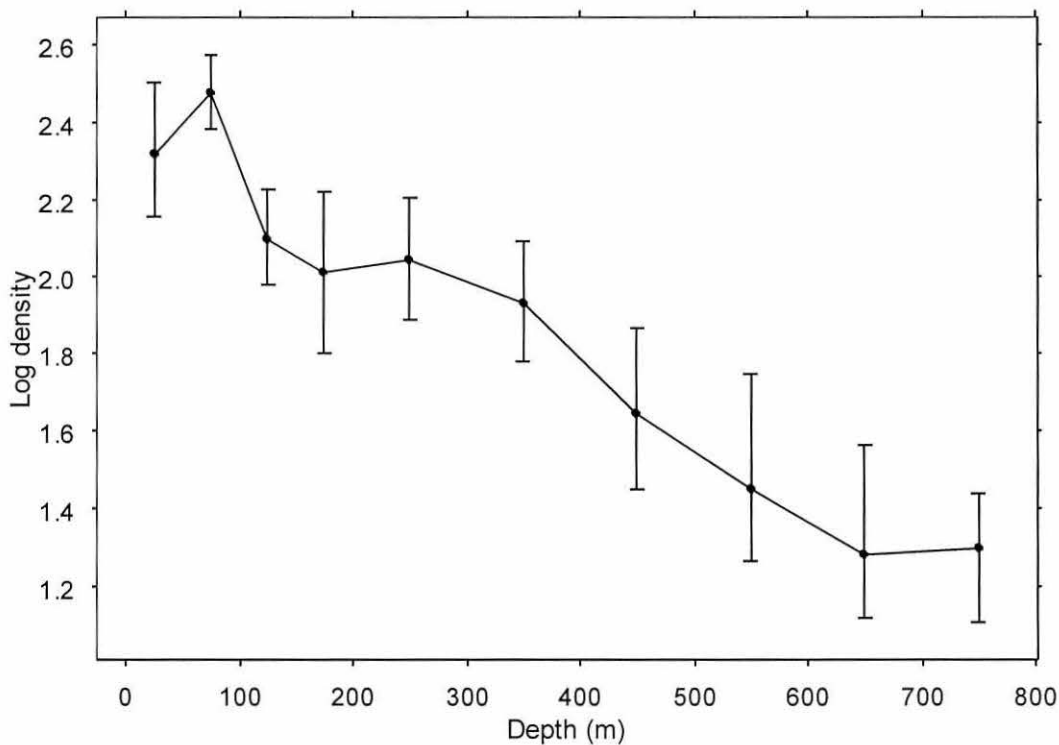
Geographical variability

Figure III-7 shows the median log$_{10}$ density (± CI$_{95\%}$) for each geographic area combined for depth and year. The pattern closely reflects that of occurrences (see Table III-2). West Alborán and Valencia show the highest median densities while East Alborán and the Gulf of Vera the least. Confidence intervals are large for all areas, not unsurprisingly since again, depth and year are compounded within the data.

Figure III-7: Geographic variation of *L depurator* median densities ($\log_{10}$(Number $\cdot$ km^2+1) $\pm$ CI$_{95\%}$), along the Mediterranean coast of Spain from all years and depths shallower 500 m. See Figure II-3 for the abreviations of the sectors.
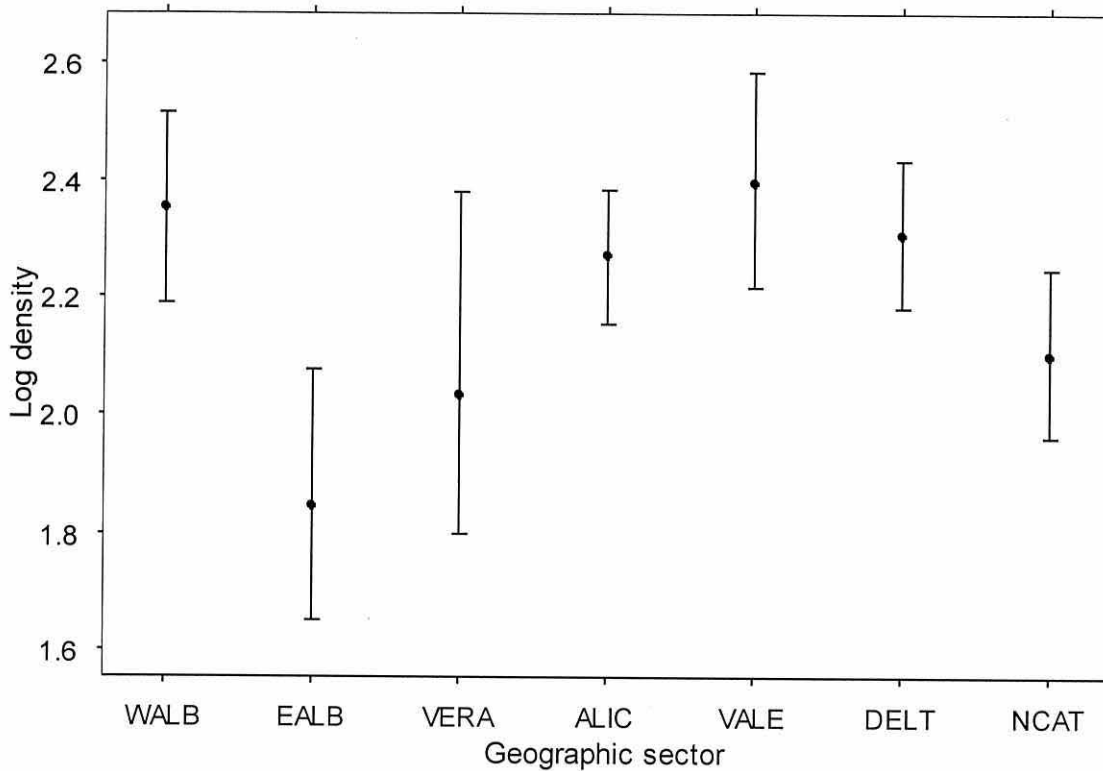
Interannual variability

Figure III-8 shows that, for most of the data, the same pattern of density distribution with depth is noticed throughout the years, with the highest densities evident between 50-150 m. Densities then decline at greater depth. When *L. depurator* are encountered at depths 200-500 m densities of around 50 crabs.km^{-2} are usual and the gradual decline indicated in Figure III-6 must result from the increasing proportion of empty trawls. In 1996, 1999, 2003 and to a lesser degree 2001, densities appear lower than average in the 50-150 m depth zone. The rather well defined peak, seen in other years, is much less evident and densities are much more evenly spread over the depth range. 1999 is the only other year showing general density reduction, both above and below the 150-200 m contour.

Overall, *L. depurator* density decreased significantly (slope= -0.12 $\log_{10}$crabs.km^{-2}.y^{-1} or a 12% annual decline in density) with year, attaining maximum average abundance in 1995 and minimum in 2003 (Figure III-9). The patterns observed were similar to those found for crab occurrences, with a density increase followed by greater decline from 1995 to 1999 (~17% annually) and from 2000 to 2003 (~30% annually). In 1996, however, decreased den-

sity in shallower water was not accompanied by decreased occurrence (Figure III-9 and Figure III-3).

Figure III-8: The depth distribution of *L. depurator* density ($\log_{10}$(Number $\cdot$ km^2+1) in each year. Samples deeper than 500 m and from the Ibiza sector were excluded.
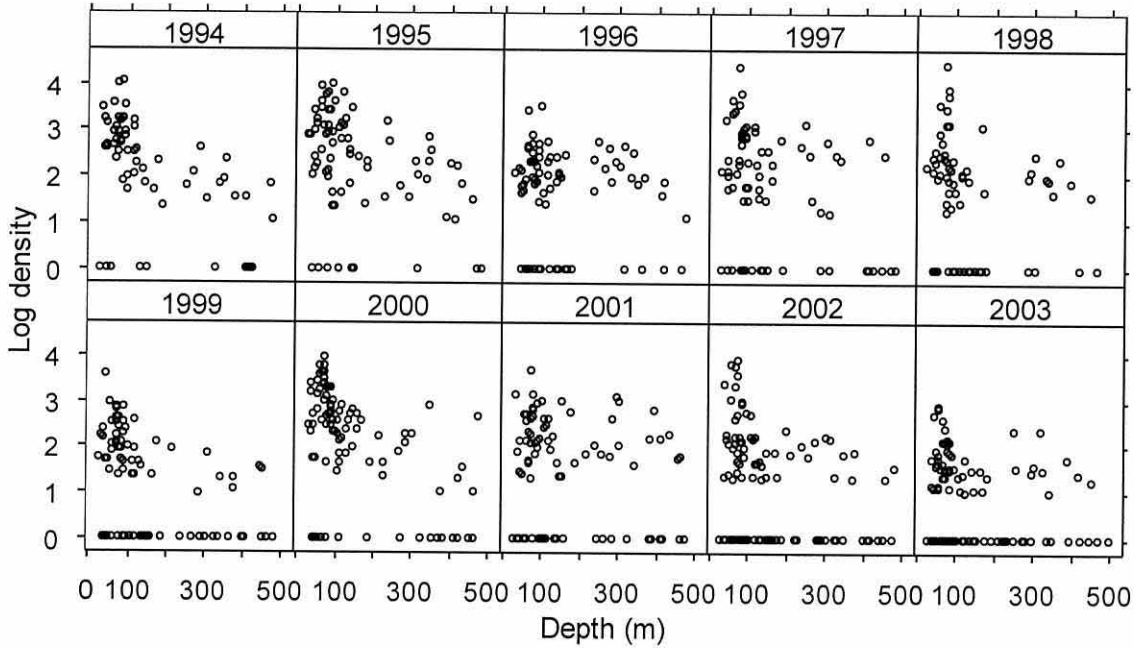
Figure III-9: Annual variation of *Liocarcinus depurator* median density ($\log_{10}$(number $\cdot$ km^{-2}+1)) ($\pm$ CI$_{95\%}$), along the Mediterranean coast of Spain.
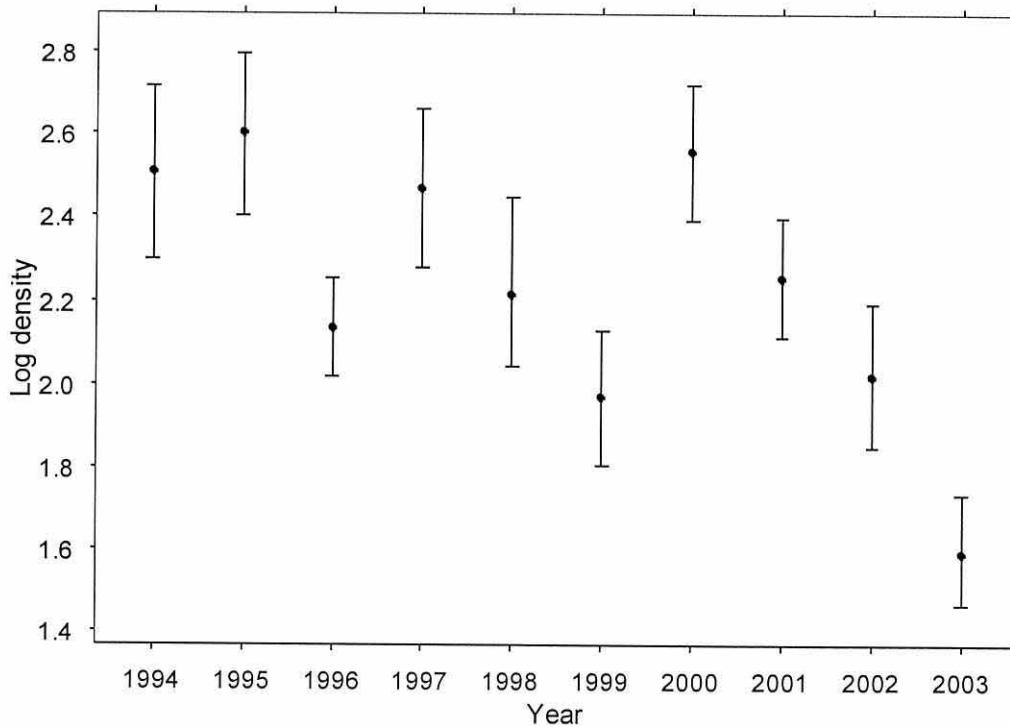
The annual variation in crab densities (excluding hauls with no crabs present) with depth is shown in Figure III-10. Although all correlations again indicate a decreasing trend, the only significant correlation was attributable to the depth range 101-150 m (Figure III-10). The lowest median densities at all depths shallower than 200 m, were evident in 2003.

Figure III-10: Annual variation of *Liocarcinus depurator* median density ($\log_{10}$(crabs$\cdot$ km^{-2})) ($\pm$ CI$_{95\%}$) at different depths (m)(only hauls containing crabs are used). The value of Kendal's tau, is indicated in the bottom left corner of each figure, followed by an * when significant. Lines fitted to significant relationships by least squares regression are merely indicative of the trend.
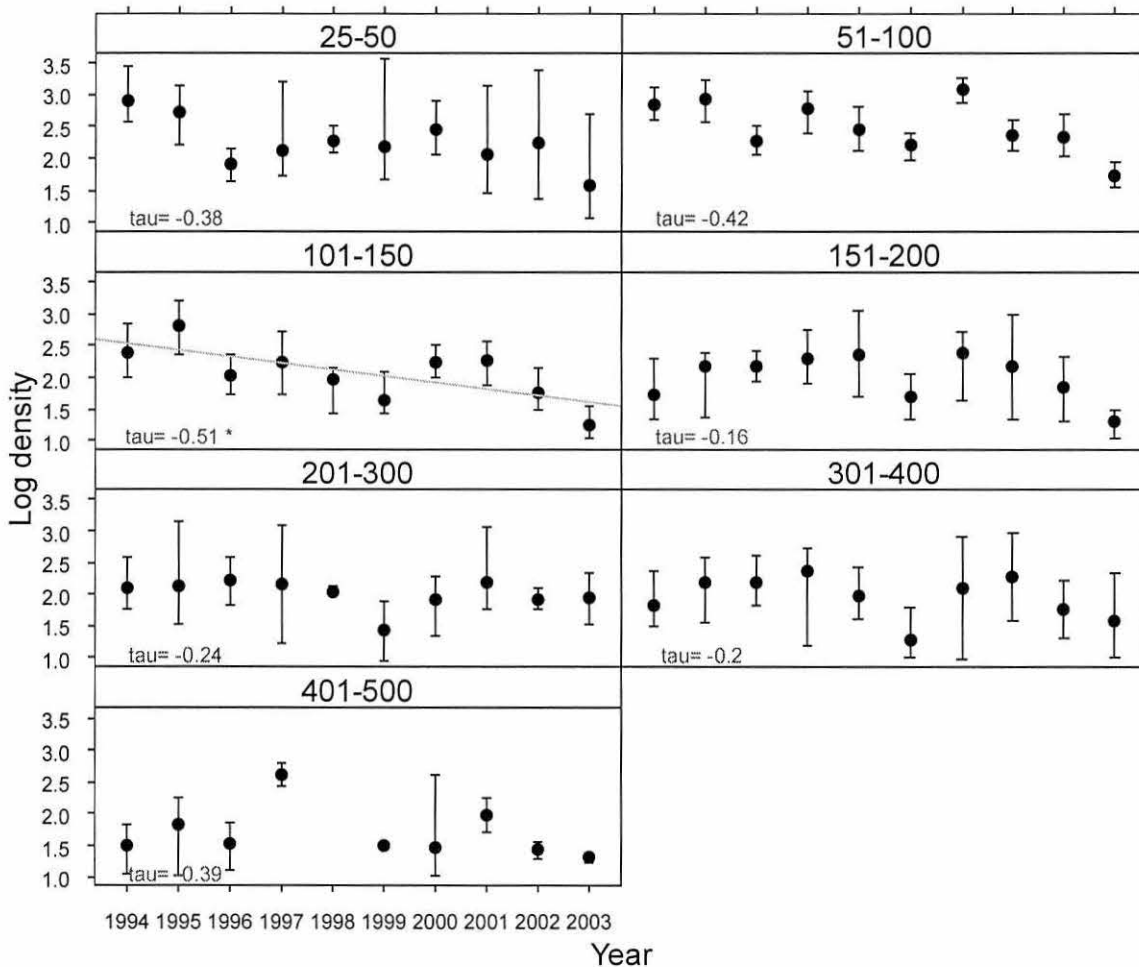
Figure III-11 shows that except in West and East Alborán, the median density in 2003 was the lowest recorded since 1994, although CI$_{95\%}$ overalap considerably (Figure III-11). In six out of the seven sectors a steady decline in median density is seen from 2000 to 2003, although Kendal's tau is only significant for crab abundance in the Valencia area. East Alborán has the lowest crab density over the 10 years (~60 crabs.km^{-2}) whilst all other areas supported densities of 150-490 crabs.km^{-2} in the 6 years from 1994 to 2000. Valencia supported the highest crab densities, and along with Alicante showed the most pronounced decline in median densities past 2000.

Figure III-11: Annual variation of *Liocarcinus depurator* median density ($\log_{10}$(number · km^{-2})) ($\pm$ CI$_{95\%}$) along the Mediterranean coast of Spain (only hauls containing crabs were used). The value of Kendal's tau, is indicated in the bottom left corner of each figure, followed by an * when significant. Lines fitted to significant relationships by least squares regression are merely indicative of the trend. See Figure II-3 for the abreviations of the sectors.
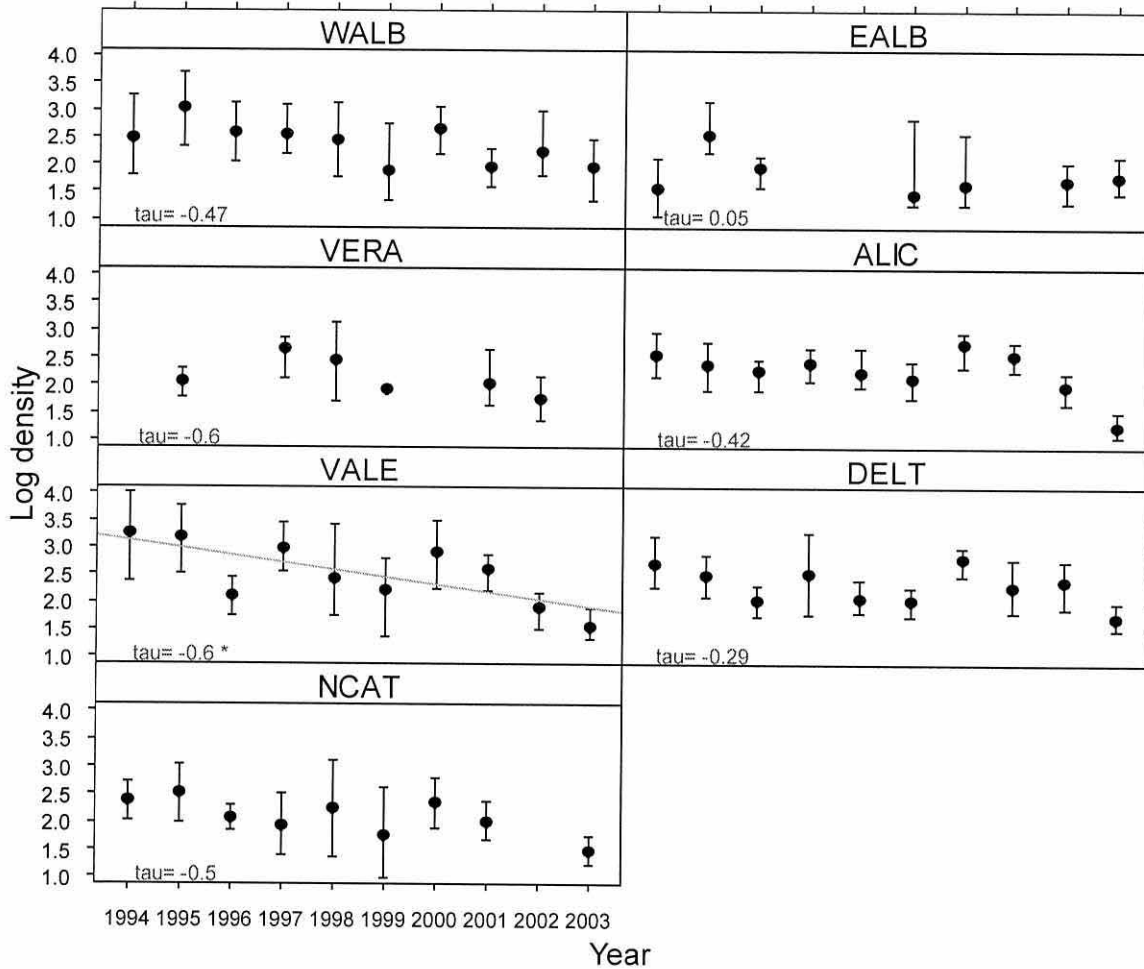
III- 5.2. Linear model of the densities

Figure III-12 shows the relationship between depth and year with *L. depurator* $\log_{10}$ densities (considering only hauls containing crabs), for all geographic locations. There is clear difference in the distribution of *L. depurator* with depth between the pattern in shallow and that in deeper waters (see Figure III-8). The distribution of density has thus been further analysed by considering the depth range < 150 m separately from that >150m. Figure III-12 shows the fit of a 'Lowess function' to the combined densities for each area and year. Despite the widely scattered points, the fitted function indicates the existence of the modal density at around 80-90 m. Below 150 m densities are fairly evenly spread to about 300 m, although the Lowess fit suggests a possible density increase at around the 300 m mark. *L. depurator* densities then de-

cline as depth increases. The two Lowess fits are suggestive of a quadratic relationship between Log density and depth.

Figure III-12: Lowess functions fitted to *L. depurator* $\log_{10}$ densities (only positive hauls) and depth (m). One function is fitted to densities at <150 m and another to those >150 m.
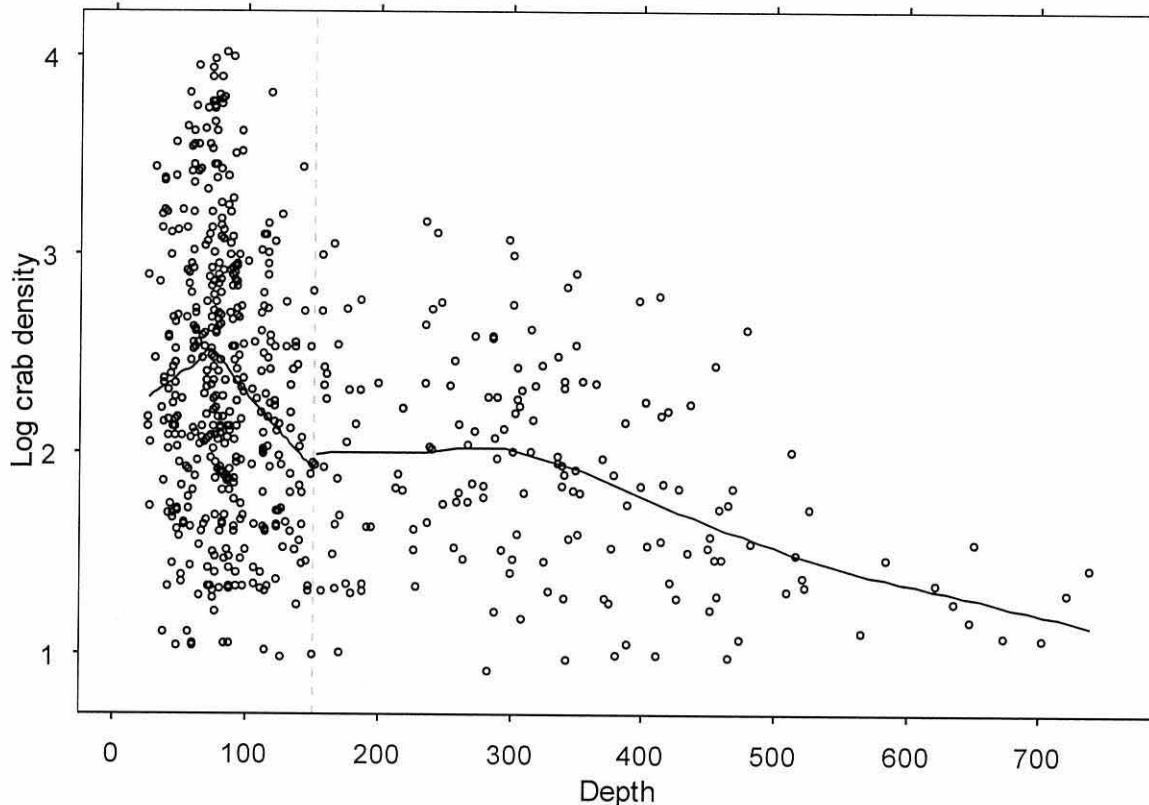
In an attempt to model changes in density with depth, year and geographic location, regression analysis was undertaken using $\log_{10}$ density as the independent variable, depth, depth squared and year as covariates and location as a fixed factor. Initial factorial analysis revealed no significant effect of location ($F_{[1,6]} = 3.01$, p = 0.008) and no significant interaction terms (F ranged from 0.79 to 1.79, p from 0.099 to 0.574) hence multiple linear models were employed to express the average impact of depth and year on *L. depurator* densities. The results are shown in Table III-5 where depths <150 m and those greater than 150 m are analysed separately. The coefficient of determination for both models was low (<150 m r = 19%, >150 m r = 22%), yet a significant proportion of the variation was explained by the fits in each case. The spread of residuals around the fitted models indicated that a quadratic fit with depth was the most appropriate model for both data sets. The decrease of *L. depurator* density from 1994 to 2003, was greater at shallower depths (~8±1%) than in deeper waters (~4+1%). Figure III-13 shows the multiple model fitted to the data for the two depth ranges. Figure III-13 c-d indicates the fit to the actual densities and indicates the peak density in shallow water to be found close to 80 m. The relationship with depth is modelled reasonably well (*cf.*

Lowess fit Figure III-12) but the representation at greater depth is less convincing (0.2% decrease per m).

Figure III-13: Multiple linear model for *L. depurator* density ($\log_{10}$ in a and b) and depth for all 10 years (1994 is the first line, 2003 the last), (a) and (c) for depths shallower and (b) and (d) deeper than 150 m. (c)-(d) detail of the density in non log form scaled (the scale has been cut at 800 and 200 crabs.km^{-2}).

(a)

(b)

(c)

(d)
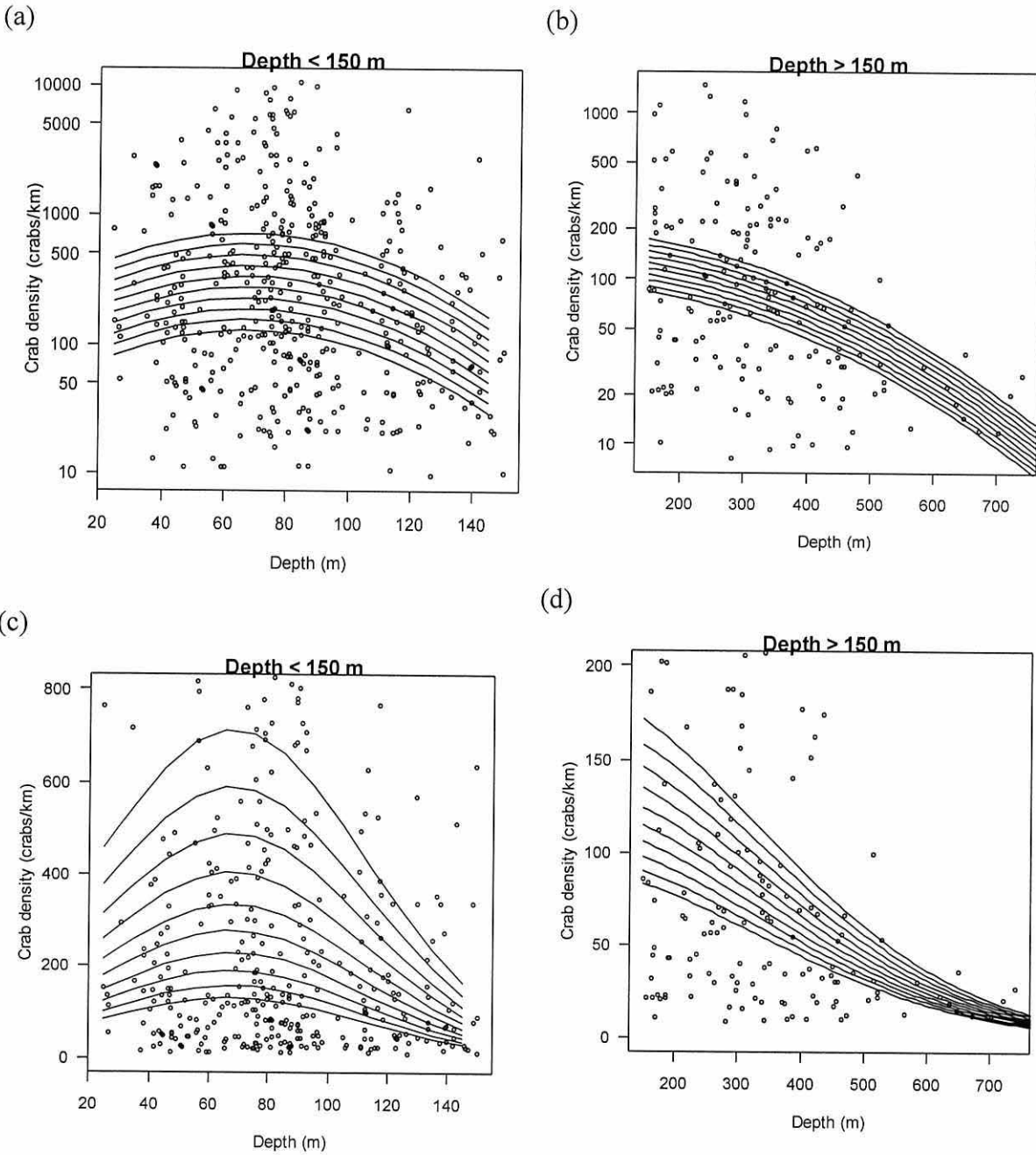
Table III-5: Summary of the multiple linear models fitted to the log densities of *Liocarcinus depurator* to year and depth.

a) Regression coefficients

	Depth < 150 m:				Depth > 150 m:			
	Coefficient	Std. Error	T	p	Coefficient	Std. Error	t	p
Intercept	166.85	21.70	7.69	<0.001	71.89	27.02	2.66	0.009
Year	-8.249×10^{-2}	1.086×10^{-2}	-7.60	<0.001	-3.491×10^{-2}	0.01352	-2.58	0.011
Depth	1.447×10^{-2}	5.827×10^{-3}	2.48	0.013				
Depth^2	-1.07×10^{-4}	3.3×10^{-5}	-3.29	0.001	-2×10^{-6}	0×10^{-6}		

b) Anova table

	Df	Adj. SS	F	p	Df	Adj. SS	F	p
Sector	6	4.2877	1.76	0.106	6	2.4641	1.75	0.113
Year	1	23.4775	57.74	<0.001	1	1.5629	6.67	0.011
Depth	1	2.5064	6.16	0.013				
Depth^2	1	4.3952	10.81	0.001	1	6.4815	27.64	<0.001
Residuals	416	169.1579			157	36.8158		

III-6. DISCUSSION

From 1994-2003 the portunid crab, *Liocarcinus depurator*, was found throughout the western Mediterranean coasts of the Iberian Peninsula from Gibraltar to Cape Creus, as noted previously by Abelló *et al.* (2002). The areas of highest occurrence were West Alborán and the region from Alicante to Delta, where the continental shelf is widest. North Catalonia had moderate densities but occurrence has sharply decreased since 2000. The regions with the narrowest continental shelf had the lowest crab occurrence, *viz.* the Gulf of Vera and the East Alborán Sea. *L. depurator* was virtually absent from the waters around Ibiza, an oligotrophic area. Although occurrences were lower in north Catalonia than in Alicante, crab density was higher. The Ebro Delta has a wide expanse of continental shelf due to the outflow of silt and clay from the river. The area also has highly productive waters boosted by the input from the river Ebro, particularly to the south where nutrients from the river are carried by the prevailing currents.

Direct comparison with previous work is fraught with difficulty since capture efficiencies vary greatly with trawl characteristics and capture methods, of which many are represented in the literature. Moreover, previous studies of *L. depurator* abundance along the Mediterranean coast of Spain were restricted to North Catalonia (coast of Barcelona and Tarragona) and the densities were reported in crabs.h[-1] trawled (e.g. Abelló *et al.*, 1988) and not

in units related to the area trawled (e.g. Galician coast: Fariña & Pereiro, 1995; Ria Ferrol: González-Gurriarán *et al.*, 1991). Abelló *et al.* (2002) found that *L. depurator* constituted about 20% (% occurrence relative to other species) of the benthic crustacean community of the Ebro Delta, Alicante and North Catalonia respectively. In the present study *L. depurator* occurrences were highest (~83 - 86% of trawls) around Valencia and West Alborán. Occurrence around Alicante and the Ebro Delta were only moderate (54 – 74%) despite constituting around one fifth of the benthic community. Occurrences around Galician coasts, at 63% of trawls taken between 100 and 500 m, were equivalent to those found around Alicante and the Ebro Delta (Fariña *et al.*, 1997).

Liocarcinus depurator was found in high densities down to about 200 m with a modal abundance between 50 and 100 m. Occurrence increases slightly deeper than 100 m but density, although lower than in shallower waters, remains fairly constant to around 400 m depth. Below that, density drops sharply and occurrence is negligible deeper than 500 m. Such reasonable density at 201-300 m, coupled with lower occurrences (i.e. % of trawls yielding crabs) would suggest that below 200 m, expanses of the muddy substrata, preferred by *L. depurator*, were plentiful. Present results agree with previous studies of depth distribution in the Mediterranean Sea, where greatest *L. depurator* densities are always found in water shallower than 100 m (Adriatic Sea Šimunovic, 1997; Ligurian Sea Mori & Zunino, 1987; South Adriatic Sea Ungaro *et al.*, 1999). On the Atlantic coast of Spain, however, highest abundances were always between 100 and 300 m depth (Galician coast Fariña *et al.*, 1997; Cantabrian Sea Olaso, 1990).

Abelló *et al.* (2002) has shown that *Macropipus tuberculatus* shares a similar depth range with *L. depurator* but their highest occurrence lies in the range 200 to 500 m with only a 30% occurrence in trawls from 100 to 200 m (Abelló *et al.*, 2002). *M. tuberculatus* has very similar habits to *L. depurator* and most probably is a potential competitor. Thus, the lower densities of *L. depurator* from 200 to 500 m may also be due, in part, to competition with *M. tuberculatus*.

Significant decrease in density was seen from 1994-2003 at all depths <150 m but no such relationship was observed at >150 m if zero occurrence is excluded. The strongest decreases seen tended to be in the 101-150 m range where high densities were not seen in most of the years following 2000. 2003 showed by far the lowest densities on average. The multiple linear analysis clearly established the prevailing trends. Density patterns in *L. depurator* were delineated by depth. The number of crabs decreased significantly from 1994 to 2003 and varied with depth, but those relationships were not significantly different between geographic locations. The annual decrease in density was most pronounced in shallower waters, where the crabs are in greatest abundance and where habitat occupancy is highest (equivalent to % occurrence in trawls). In deeper water occupancy changes more noticeably over the 10 years which is, on average, reflected in lower densities. When zero occupancy is ignored average densities at depth do not show the

marked annual decrease. The multiple linear approach does not take into account the superimposed annual trends in density evident, for example in Figure III-9, where a potentially cyclical trend in *L. depurator* population density may be emerging. Thus the average densities predicted from the multiple model for 1999 are higher than those predicted for 2000 even though the actual densities measured in 2000 were considerably higher than those measured in 1999. A large part of the unexplained variance in the multiple models undoubtedly derives from this potential cyclical trend with a possible 3-4 year periodicity. Furthermore, variability, which is inherent to location, is also difficult to estimate since no record of bottom sediment type or condition was made for each trawl. Since muddy substrata are preferred by *L. depurator* the ratio of the area of preferred to that of 'other' substrata in the trawl path would help explain more of the vast variability seen in the current data.

IV. Geostatistics

IV-1. SHORT INTRODUCTION TO GEOSTATISTICS

This chapter aims to provide a short, non-mathematical, introduction to the main aspects and practical considerations of basic geostatistics. An extensive description of the mathematical basis for geostatistical techniques can be found in Cressie (1991), Rivoirard *et al.* (2000) and Webster & Oliver (2001).

IV- 1.1. Why perform a geostatistical analysis

At large scales, animals are not generally randomly distributed in space (Koenig, 1999). Their distribution is usually clustered into patches dependent on the heterogeneity of the environment, the organisms, physiology and mode of life. For example, if the main prey item of a particular species is aggregated in 3 km^2 patches because of environmental heterogeneity then the predator is also likely to be clustered in similar 3 km^2 patches. Furthermore, if you are standing in the centre of the patch (maximum density values) and walk towards its edge you would expect the abundance of the organism to decrease (either smoothly or abruptly) as the edge of the patch is approached. Beyond the edge of the patch both organisms would be very rare or absent. The manner in which density decreases, from the centre to the edge of the patch, can be modelled by means of a spatial correlation function. This model, called the spatial covariance model, is often estimated from a variogram that describes the variance in abundance in relation to distance between measurements of abundance.

So, once density measurements (discrete sampling) have been obtained over an appropriate spatial scale (for the question posed), the experimental spatial covariance model (known as the "experimental variogram") can be calculated. The experimental variogram is employed to build a spatial model that provides a continuous representation of how the species is distributed in space, defining the extent of patchiness in abundance. Models can be compared between sites, population classes (e.g. juveniles, females) or species.

Species generally occupy the entire area and are not restricted to the sampled locations. Thus, although individuals may well be continuously distributed in space, sampling is always discrete. Through the study of the spatial structure, it is possible to produce a map of the population density with estimates of the species abundance at unsampled locations, producing a continuous map (through an interpolation technique such as kriging).

Spatial autocorrelation arises when the estimated value of abundance at one sample location is very similar to the value of neighbouring abundance but less similar to those at some distance away, i.e. the spatial co-ordinates of the samples determine how similar the samples should be (among others Cressie, 1991; Koenig, 1999).

In its simplest form, a geostatistical analysis assumes that the abundance of an organism (the response variable) is relatively constant over the sampled area and that the variance of abundance measurements is approximately constant (Cressie, 1991; Maynou *et al.*, 1998). This is called the second order stationary assumption in geostatistics. If the assumption is not met, then more complex models can be sought, by adding ancillary information to stabilise the variances or equalise the abundance or geography, for example. Decreasing trends with depth can be included directly in the contouring method (e.g. kriging with a trend) or by inclusion of one or more covariate(s) in the production of the spatial model (e.g. universal kriging or kriging with an external trend). The second order stationarity assumption is investigated with an exploratory data analysis (e.g. looking at the graphs of density/North and density/East) (Chilès & Delfiner, 1999; Cressie, 1991; Maynou, 1998; Rivoirard *et al.*, 2000; Webster & Oliver, 2001).

Geostatistical analysis is most efficient when the abundances are normally distributed (Rivoirard *et al.*, 2000). Skewness and the presence of outliers, so common in biological data makes the estimation and production of a variogram difficult, and may obscure any spatial structure in the data. Data transformation to approximate normality can help, but the result is always approximate in the arithmetic scale and a particular back-transformation procedure is required (e.g. log-normal kriging). Fortunately, geostatistics are relatively robust to departures of normality (Cressie, 1991).

IV- 1.2. Variogram analysis

Experimental variogram

Figure IV-1 describes the production of an 'experimental' variogram from a set of simulated data points distributed north and east (Figure IV-1a). As an example, consider only two sample points (point I and II), with their respective spatial co-ordinates (North and East) and the value of the measured variable at those points (e.g. crab density). The covariance (the squared difference of the densities) and the Euclidean distance between the two points is calculated. Such is done for all pairs of sample points and the variogram cloud (Figure IV-1b). If the points in the variogram cloud are grouped into distance intervals, the 'experimental' variogram (more correctly semivariogram, when half the covariance is used) appears as the aver-

age covariances within each interval (Figure IV-1c). The number of classes, can be determined by dividing the distance (xx axes) into n segments or by dividing the points into n groups. In both cases, these groups are named lags or bins.

Figure IV-1: Example of a simulated data set of 100 points (a) location of samples and density magnitude (proportional to circle diameter) (b) variogram cloud. (c) experimental variogram derived from 0.1 km segments of the separation distance axis.
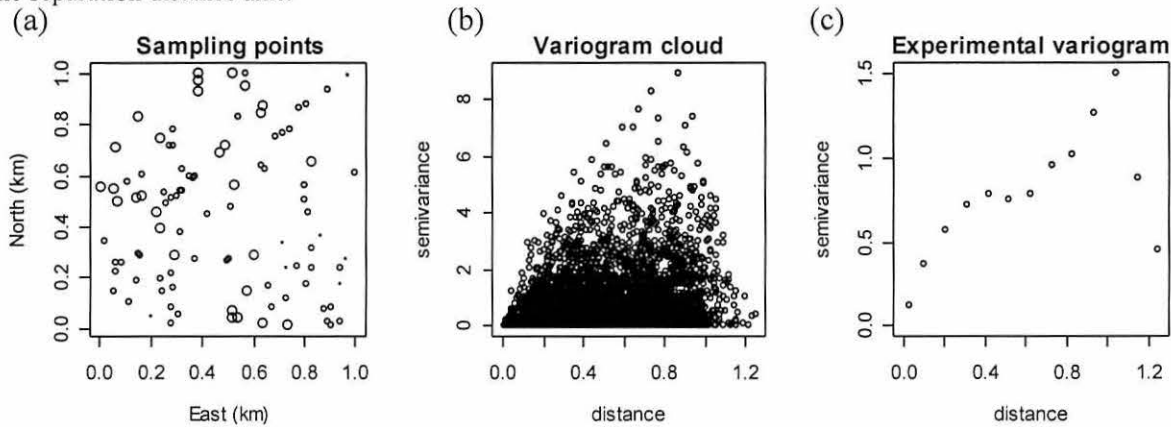
There are several variogram estimators (formula used to produce the variogram) available in the literature, although the 'Classical estimator' (used in most geostatistical software), and the 'Robust estimator' are probably the most common. To calculate the 'Classical' (experimental) variogram, the variogram cloud is divided into N classes (bins or lags) and the mean point within each class is plotted (Figure IV-1; eq. 1). When estimating the 'Robust' variogram (Cressie & Hawkins, 1980; Cressie, 1991), the medians within each class are calculated, so that the variogram is more robust to departures from normality and the presence of outliers in the data distribution.

$$\gamma * (h) = 0.5 \frac{1}{N(h)} \sum_{N(h)} \left[Z(x_i) - Z(x_j) \right]^2 \quad \text{eq. 1}$$

where $N(h)$ is the number of pairs of points, separated by the vector distance h. γ^* represents the semivariance (ploted in the y co-ordinate of the experimental variogram graph). Z represents, crab density at locations xi.

A major component in the resolution of variogram calculation is the number of distance classes used (i.e. the number of bins). This choice is usually based on visual criteria, although forms of 'nearest neighbour' analysis can give a hint on the decision (Figure IV-2 and Figure IV-3).

Figure IV-2: Experimental variograms produced with increasing resolution of the distance measure (classes, lags or bins), from 5 to 34.
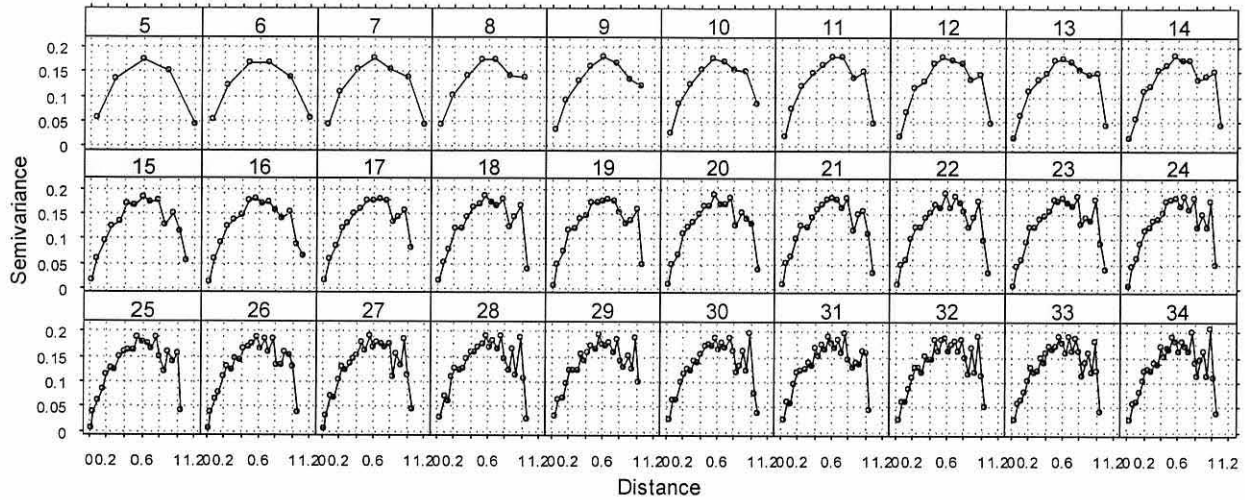
Figure IV-3: Using the data and the variograms in Figure IV-2, variation in the fitted parameters, using weighted least squares (WLS) with the number of classes used. The nearest neighbour analysis is the frequency of paired points separated by a certain distance and the higher frequency number of classes advises on the most appropriate resolution to adopt.
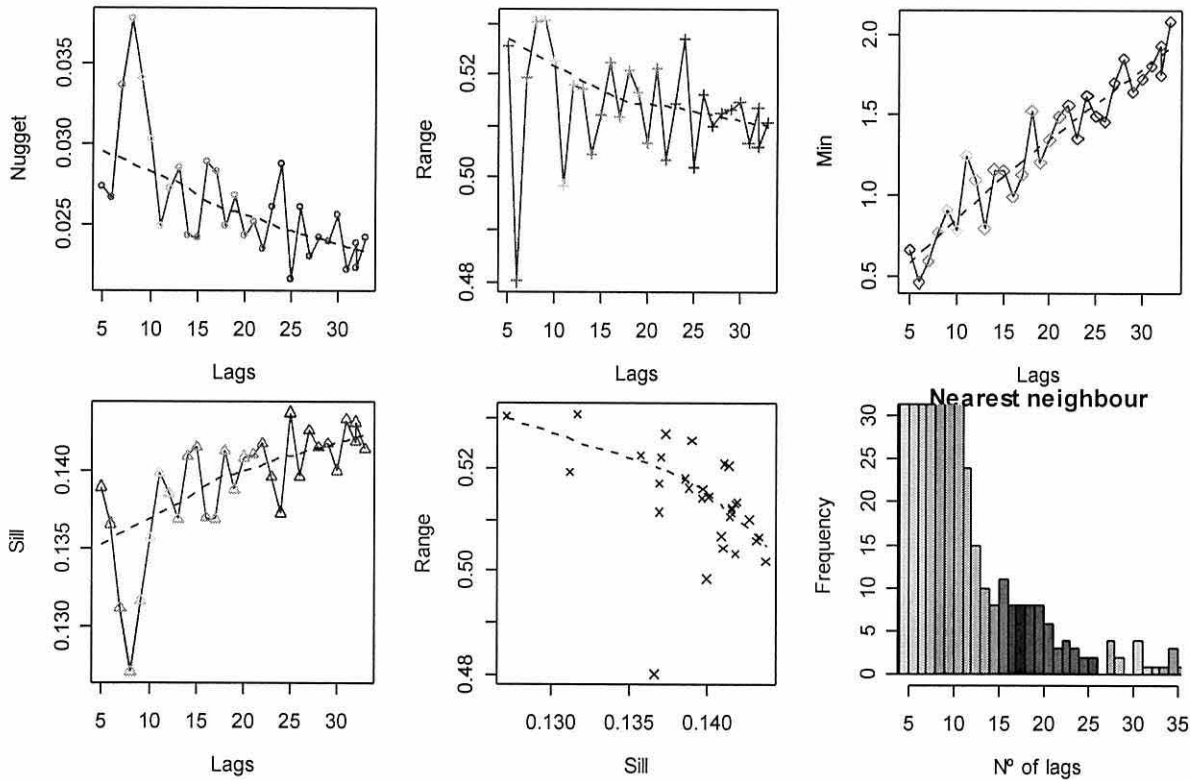
IV- 1.3. Spatial covariance model parameters

Once the variogram is constructed, a function (the spatial covariance function or variogram model) is fitted to the relationship of the covariances and distance. The nature of the relation-

ship must clearly fit the shape of the variogram. The spatial covariance model is expressed by three parameters: nugget (indicates the variance not explained by the spatial model), sill (the sill indicates the variance explained by the spatial model)(note that some authors name the 'sill', as the total variance and the 'partial sill', as the variance minus the nugget whereas others (as in the current thesis) consider the term 'sill' as the 'partial sill') and range (interpreted as patch size in ecological studies by Sokal, 1979)(Figure IV-4).

The nugget represents the behaviour of the variogram at the origin, which reveals the degree of spatial continuity or regularity of the variable (Rivoirard *et al.*, 2000)(Figure IV-4). At zero distance there can be no variation in abundances so if a model defines a significantly positive semivariance at zero it must result from inconsistent variability that is not explained by the general fit. Maynou *et al.* (1998) consider the presence of a nugget effect to indicate micro-scale variability at distances shorter than the smallest distance between sampling locations however, a nugget effect could also indicate sampling error or random noise. The presence of a nugget effect can considerably increase the difficulty in fitting the variogram model. Sampling at intervals appropriate to the spatial heterogeneity may reduce the nugget effect. However, this implies some fairly detailed knowledge of that heterogeneity prior to sampling, a luxury not often afforded in most biological sampling programs. In the absence of spatial autocorrelation, the experimental semivariogram, would appear flat, indicating no correlation between distance and variance (Maynou *et al.*, 1998).

Figure IV-4: Nugget sill and range of the variogram. The black line in bold, shows the variogram model (spatial covariance model), the words with in bold indicate the terms mentioned in the text.
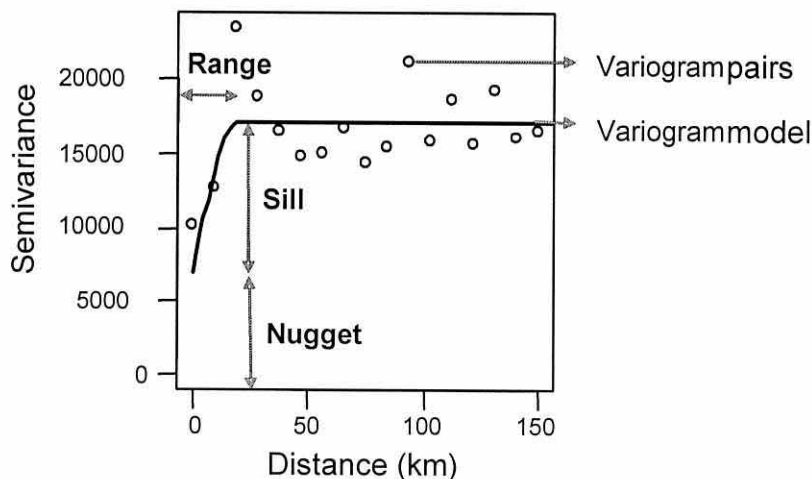
The sill (or partial sill) (plus any significant nugget) corresponds to the total variance in abundance measurements (Figure IV-4). The percentage of spatial dependence, which represents the variance explained by the model, is given as the partial sill as a percentage of the sill ([1- (nugget/sill)]×100).

The range represents the distance beyond which no effect of the spatial covariance among samples can be demonstrated (Maynou *et al.*, 1998) and hence corresponds to the extent of the patch of organisms sampled (Sokal & Oden, 1978)(Figure IV-4).

IV- 1.4. Spatial covariance model function

The selection of an appropriate model should initially be done with respect to variogram shape. Fully automatic model choice by direct application of fixed criteria has been proposed (e.g. GOF in Rivoirard *et al*, 2000) but such rigidity is not always warranted or desirable. Figure IV-5 shows the commonest types of functions that have been used in variogram fitting. In the exponential, Gaussian and spherical models the range is interpreted as patch size, whereas in the linear model the density would be always increasing throughout space possibly representing simply a gradient. Figure IV-6 shows examples of the practical differences in contour mapping arising from fitting different functions to the variogram

Figure IV-5: Common variogram models (examples obtained from Surfer 8- Golden Software inc).

Exponential Model   **Gaussian Model**

Spherical Model   **Linear Model**
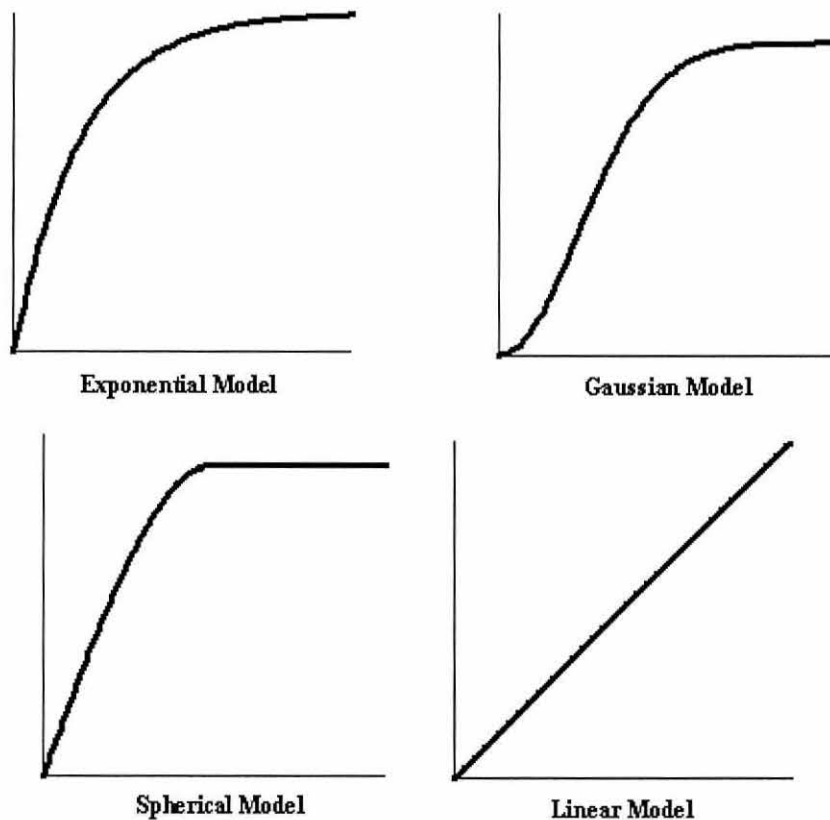
Figure IV-6: The effect of spherical, exponential, gaussian and linear variogram models fitted by weighted least squares (WLS) to the same simulated set of 100 randomly generated abundance points, (with known spatial structure: sill of 0.3 and a range of 0.5). a) Distribution of simulated sampling points (the diameter of the circles is proportional to the value of the abundance). b) Experimental variogram and different spatial covariance models (results were: spherical (n=0.02; s=0.13 ; r=0.51), exponential (n=0 ;s=0.17 ; r=0.18), Gaussian (n=0.04; s=0.12; r=0.24) and linear (a=0.10;b=0.08); note that in the spherical model the estimated range corresponds to the actual range, while in a Gaussian model actual range =range*sqrt 3 and in the exponential model, actual range=range*3 (Cressie, 1991). c) kriging estimated contour maps of abundance derived from each model.

a)

b)

c)
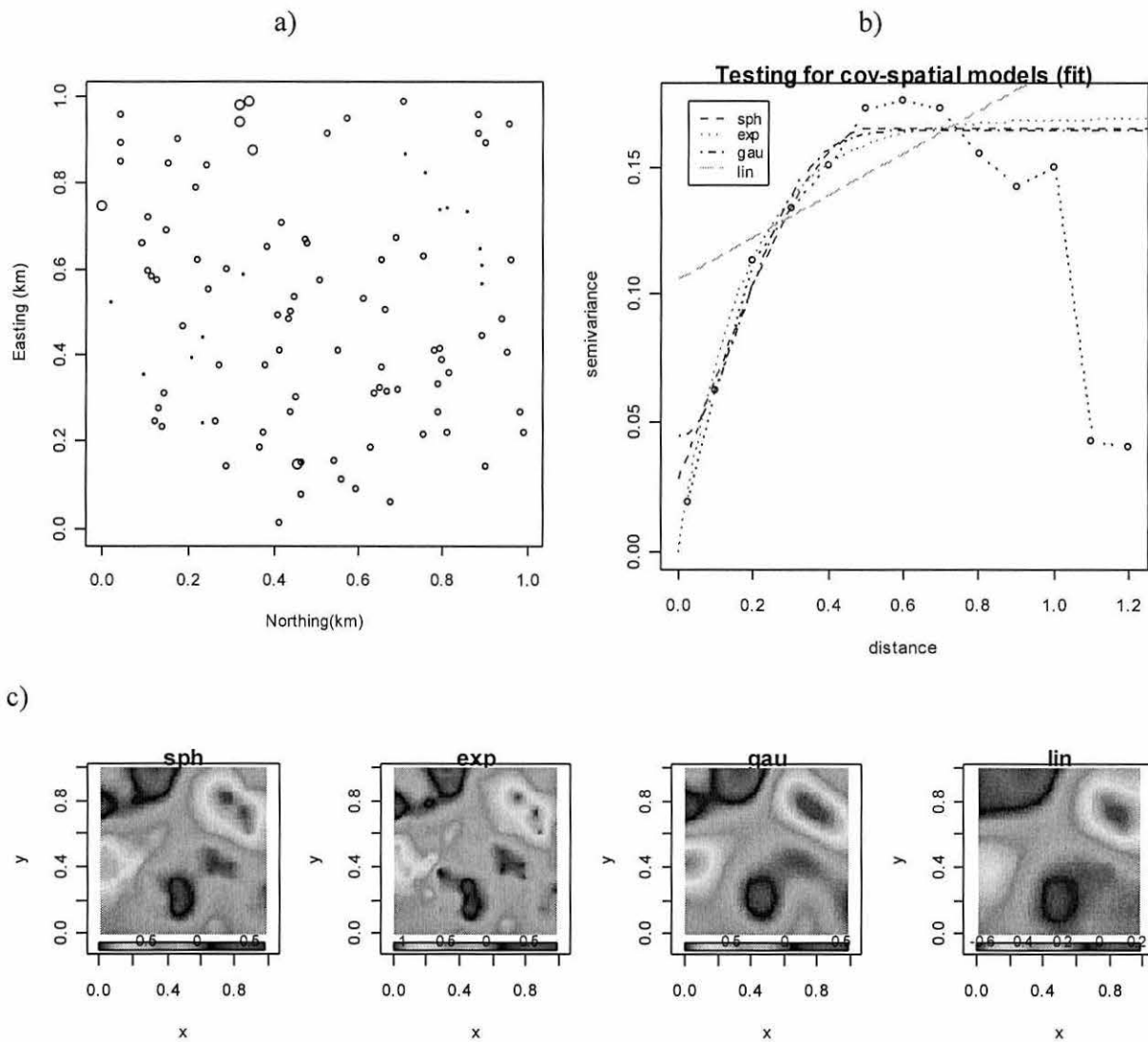
IV- 1.5. Fitting method

A fitting method is used to estimate the parameters of the spatial covariance function found in the variogram. The simplest fitting method is the Ordinary Least Squares (OLS), where the selected covariance model (e.g. spherical, gaussian, exponential) is fitted, minimising the squared distances to the experimental variogram points. OLS has been criticised for giving the same weight to distance classes irrespective of the number of points in the class. The Weighted Least Squares (WLS) method, where the number of pairs in a bin is used to weight

the fit, has been commonly employed and recommended. A comparison between different fitting methods using the same variogram and assuming the same spatial model is shown in Figure IV-7. Whatever the fitting method used, the largest distances are not considered in the fitting procedure, and thus are often omitted (Journel & Huijbergts, 1978, 1978 recommend using only the first half or 2/3 of the distance classes). Fitting "by eye" alone gave similar results to the other methods. This is logical, since all variogram models are fitted interactively and hence require reasonable estimates of the initial parameters. Fitting "by eye" is an essential pre-requisite to choosing the initial parameters that are then "fine-tuned" by the curve fitting procedure.

Figure IV-7: The effect of different fitting methods (OLS, WLS and Cressie) in the spatial models parameters (nugget, sill and range), for a spherical model fitted to the same experimental variogram and using the same data. Original data is a simulated set of 100 random autocorrelated samples with spherical covariance model, (sill of 0.3 and a range of 0.5). The first graph shows the experimental variogram and the models estimated with different methods (OLS: dashed line; WLS: dotted line and Cressie (another fitting method) dot-dashed line), always assuming a spherical model. The remaining figures, are contour abundance kriging estimated maps of the sampling area, using the resultant spatial models.
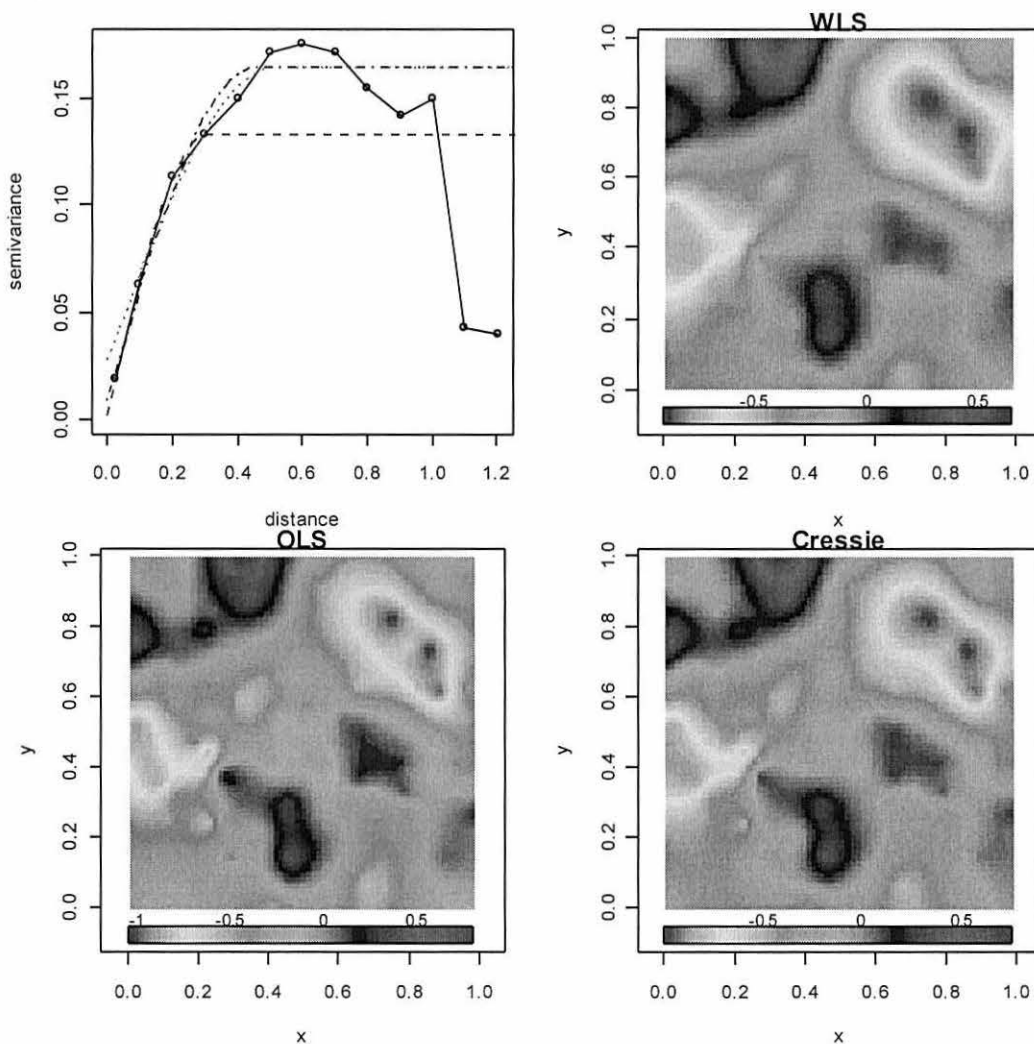
IV- 1.6. Kriging interpolation

In producing contour maps of any variable distributed in two or three dimensions, it is always problematic to find appropriate interpolations between samples. If the area has been 'under-sampled' the problem increases in difficulty. Kriging is an 'exact interpolator' (at the sample location, the kriged value equals the sampled value, except when there is a nugget effect, which determines the possible variation of the value around the sampled one), which presents certain statistically optimal properties, unlike other interpolators. Perhaps the most important one for biologists is that it provides measures of the error or uncertainty of the estimates, that are produced by minimising the error (Rivoirard *et al.*, 2000). As a function of the model selected, best linear unbiased estimates ('BLUE') are calculated for the average density and their estimated variance over any region of interest. Table IV-1 shows a summary of the main types of kriging commonly used.

Table IV-1: Types of kriging, with a brief explanation and some references.

Kriging type	Summary	References (Details/ Examples*)
Simple kriging	It is the simplest kriging type. It is rarely used, as it assumes that the mean is known.	Webster & Oliver (2001)
Ordinary kriging	It is the commonest type of kriging (it would be something like 'default' when nothing is specified). The local mean is considered unknown but stationary, and it is estimated by minimising the error	Webster & Oliver (2001)
Universal kriging (kriging with external trend)	The local mean is not stationary throughout the studied area, and it varies with a measured covariate, so that the estimates depend both on the variable and on the covariate. It is based on the computation of the variogram of the residuals between the variable and a covariate. The covariate may be one of the coordinates (x or y) or an external variable. The relationship with the covariate may be linear or quadratic.	Webster & Oliver (2001)
Indicator kriging	The continuous variable is converted into binary data (reduced to zeros and one)-indicators. It is a non-linear and non-parametric technique, which can be applied to virtually all distributions. This technique provides probabilities.	Webster & Oliver (2001) Goovaerts (1997; 2001) Lloyd & Atkinson (2001)
Disjunctive kriging	It is also non-linear (the non-linear function is approximated by L'Hermite polynomials), it estimates the probabilities of exceeding a certain threshold value.	Webster & Oliver (2001) *Maynou *et al.* (1998) *Lembo *et al.* (2000a)
Ordinary co-kriging	It is an extension of ordinary kriging to two variables (multi-variate case). It is often applied in the cases where one of the two variables is difficult and expensive to sample, while the other is easier, so that we can obtain a good cover of sampling points throughout the area of the sample variable, and want to know the distribution of the not-so-well sampled variable	Webster & Oliver (2001) Isaaks & Srivastava (1989) *Lembo *et al.*(1999)
Bayesian kriging	It is based on the Bayesian approach, and so requires some previous knowledge on the data distribution (and drift). The kriging equations are those of the simple kriging, but assuming non stationary covariances	Webster & Oliver (2001) Chilès and Definer, (1999) *Brierley *et al.* (2003)

Examples are indicated with *

Figure IV-8: Summary of the steps in a classical geostatistical analysis.

Exploratory Data Analysis

Are the data autocorrelated?
→ Mantel test
→Variogram analysis
→Variogram envelope

Is there a trend within the sampled area?
→Linear model
→Graphs of the variables with the coordinates and covariant

Are the data normal distributed?
→Normality test (Shapiro, etc.)
Box-Cox family transformations

Variogram Analysis

How many lags?
→Visual analysis
→Nearest neighbour analysis

Which spatial model?
→Decision criterium (minimising function, gof, etc.)
→Previous experience
→Visual analysis

Which fitting method?
→OLS, WLS, etc.

Variogram of the residuals?

Variogram of the transformed variables?

Kriging Interpolation

What type of kriging?
→Ordinary kriging
→Block kriging
→Indicator kriging

What size are the estimated cells?

IV-2. GEOSTATISTICAL ANALYSIS APPLIED TO CRUSTACEANS

IV- 2.1. Historical perspective

In the 1960, Matheron invented Geostatistics and denoted a certain interpolation technique as *kriging* in honour of Krige, a South African mining geologist. The use of variograms and advanced interpolators were developed initially for the mining industry, to locate gold clusters.

In mid 1980 the first application of geostatistics to contouring the distribution of a marine species was published (Conan, 1985). To overcome the problems of applying traditional stock estimation techniques in autocorrelated samples, Conan (1985) applied kriging methods to obtain unbiased estimates of Canadian shellfish stocks. Within the field of Marine Biology, most appli-

cations of geostatistical analysis have been in fisheries surveys, both bottom trawl and acoustic, and largely for commercial species. Recently, increased computing power has led to an increase in the complexity of spatial analyses attempted (*Clupea harengus* in the North Sea, Beare *et al.*, 2002; mackerel ichtyoplankton, Bez & Rivoirard, 2001; review, Petitgas, 2001; fish schools, Petitgas *et al.*, 2001; *Melanogrammus aeglefinus* in the North Sea, Rivoirard & Wieland, 2001).

IV- 2.2. Crustaceans

In the Atlantic Ocean, two main areas have been investigated: the Spanish coast (Galician coast) (Freire *et al.*, 1991b; Freire *et al.*, 1993; Freire *et al.*, 1992; Freire *et al.*, 1991c; González-Gurriarán *et al.*, 1993) and the Canadian coast (Conan *et al.*, 1988a; Conan *et al.*, 1988b; Simard *et al.*, 1992). In the Mediterranean Sea, the areas studied cover the Catalan Sea (Conan *et al.*, 1994a; Maynou, 1998; Maynou *et al.*, 1996; Maynou *et al.*, 1993; Maynou & Sardà, 1997; Maynou *et al.*, 1998), the Adriatic Sea (Ungaro *et al.*, 1999b), the Tyrrhenian Sea (Lembo *et al.*, 1999; Lembo *et al.*, 2000a) and the Ionian sea (Lembo *et al.*, 2000b).

As might be expected of a technique for mapping resources, the crustacean species distributions analysed by means of geostatistical techniques, have always been economically important fisheries resources or associated species. In the Mediterranean, the main crustacean fisheries mapped were the *Nephrops norvergicus* (Norway lobster) (Conan *et al.*, 1994a; Maynou, 1998; Maynou *et al.*, 1996; Maynou *et al.*, 1993; Maynou & Sardà, 1997; Maynou *et al.*, 1998), *Aristeus antennatus* (red shrimp) (Lembo *et al.*, 2000b; Maynou *et al.*, 1996; Maynou *et al.*, 1993) and *Parapenaeus longirostris* (deep-water rose shrimp) (Lembo *et al.*, 1999; Lembo *et al.*, 2000a). In Canada, the distribution of *Pandalus borealis* (northern shrimp) (Simard, 1991a; Simard, 1991b; Simard & Benoît, 1992; Simard *et al.*, 1992; Simard & Marcotte, 1993), *Chionoecetes opilio* (snow crab) (Conan *et al.*, 1994b; Conan *et al.*, 1988a; Conan *et al.*, 1988b), *Paralithodes camtschaticus* (red king crab in Alaska) (Vining & Watson, 1996) and *Eriocheir sinensis* (Chinese mitten crab) were studied through geostatistical methods.

The majority of previous studies were based on linear geostatistics (e.g. Freire *et al.*, 1991b; Freire *et al.*, 1993; Freire *et al.*, 1992; Freire *et al.*, 1991c; Maynou *et al.*, 1996; Maynou *et al.*, 1998; Ungaro *et al.*, 1999b). Lembo *et al.* (1999; 2000a) used co-kriging, with depth or the preceding year density estimates as an auxiliary cross-correlated variable, to map the distribution of *Parapenaeus longirostris*. The distribution was then extended temporally into the following year (Lembo *et al.*, 2000a). Disjunctive kriging was used to help identify the location of nursery areas, of greatest recruit abundance (Lembo *et al.*, 2000a), of greatest percentage of

females larger than median size (Lembo *et al.*, 2000b) and of potentially profitable shrimp fishing areas (Maynou, 1998).

The application of geostatistical analysis to randomly stratified bottom trawl sampling of crustaceans, was first attempted by Freire *et al.* (1991b; 1992; 1991c) for the Galician coast (Atlantic coast of Spain) surveyed in 1983/84. They showed the existence of a well-defined spatial structure for the main crustacean by-catches (Fariña *et al.*, 1992; Freire *et al.*, 1991b; Freire *et al.*, 1992; Freire *et al.*, 1991c; González-Gurriarán *et al.*, 1993).

Sobrino & Garcia (1993) showed a clear spatial structure to the population of Penaeus notialis in Mauritania, throughout the year. However, the variograms were less defined from August to October showing a more complex spatial structure. Ranges varied from 60 to 113 km (Table IV-2). Both parameters could be separated into one of greater abundance from August to January, which corresponded to higher biomasses, and the other for the remaining months with lower abundances. Sobrino & Garcia (1993) observed an increase of the patch size in relation to density. Furthermore, two distinct populations were identified, one in the north of the sampling area and the other in the south. By using geostatistics these author reduced by 25% the standard deviations of biomass estimations (Sobrino & Garcia, 1993).

Table IV-2 shows a summary of most applications of geostatistics to crustacean populations. Conan *et al.* (1994b) tested and created a kriging algorithm that incorporated natural, environmental boundaries and then used the interpolated values as abundance and biomass for the snow crab fishery. Maynou *et al.* (1996) surveyed the nine most abundant crustacean species from a regularly spaced grid (randomly sampled within each area) trawl survey in a *Nephrops norvegicus* fishing ground off Barcelona (Spain). The results showed that the species were distributed in high-density patches, with certain pairs of species adopting mutually exclusive areas (e.g. species 1 and species 2). Species distributions were also segregated by depth. Patch occurrence was related to the presence of a submarine 'canyon' and the peculiar hydrograhic and sedimentary characteristics thus generated (Maynou *et al.*, 1996).

Maynou (1993) and Maynou *et al.* (1996) further, showed that the patch size (estimated range of the variogram model) decreased from the spring to autumn in *Solenocera membranacea*, *Sergestes articus*, *Plesionika heterocarpus*, *Plesionika martia* and *Nephrops norvegicus*, while remaining constant for the other four species (Table IV-2). These authors found that the location of the high-density areas of some species changed from spring to fall (Maynou *et al.*, 1996; Maynou *et al.*, 1993; Maynou *et al.*, 1998).

Table IV-2: The application of geostatistics to crustacean distributions. Kriging type refers to contouring only.

Reference	Species	Area	Variable	Year	Season/month	Variogram max distance	Kriging type	covariance model	Nugget	Sill	Range
Conan et al. (1988a)	Chionoecetes opilio	Canada	kg.h^{-1}	1987	July/August	30	Point K Block K	Sph	0.86	1.3	5.7 km
Sobrino & Garcia (1993)	Penaeus notialis	Mauritania	kg.h^{-1}	1967	all	160-300	OK	Sph	0-40	50-190	60-113 km
Lembo et al. (1999)	Parapenaeus longirostris	Italy (Tyrrhenian Sea)	kg.Km^{-2}	1995 1996 1997	October	90 (150)	CoK (depth)	Sph	?	?	? 17.42 10.69
Lembo et al. (2000a)	Parapenaeus longirostris	Italy (Tyrrhenian Sea)	n.Km^{-2} (recruits)	1996 1997	October	125 0-90	Disjunctive K	Exp	?	?	16.03 19.94
Lembo et al. (2000b)	Aristeus antennatus	Italy (Ionian Sea)	kg.Km^{-2}	1994 1995 1994/95	November May	140	OK CoK (year)	Exp	0 0 0	298.5 3937 39.46	26.6 22.1 35.1
			n.Km^{-2} (% large females)	1995	May	140	Disjunctive K	Exp	0	373.5	26.6
Maynou et al. (1996)	Aristeus antennatus	Spain (Barcelona)	n.Km^{-2}	1991	Spring Fall	50 km	Point K	Sph	100/0	1200/1300	7.5
	Calocaris macandreae								0	11/5	6.0
	Nephrops norvegicus								0.4/0	2/2.1	12/7.5
	Pasiphaea sivado								0	5/4	5.5
	Plesionika heterocarpus								0	25000/15	12/7.5
	Plesionika martia								1/0	2/2.2	10/7.0
	Processa nouveli								2/3.7	2.5/3.7	13.5/7.0
	Sergestes arcticus										

(Table IV-2 cont.)

Reference	Species	Area	Variable	Year	Season/month	Variogram max distance	Kriging type	covariance model	Nugget	Sill	Range
	Solenocera membranacea								3/80	2/220	16/12
	Diversity index								0	0.6/0.4	6/5.5
Maynou et al. (1998)	Nephrops norvegicus	Spain (Barcelona)	n.km^{-2} (Juv..M)	1991	Spring	50	Point K	Sph	0.4	3.9	5.9
			(Juv.F)						1.3	1.1	6.7
			(Adult M)						0.7	1.1	8.3
			(Adult F)						0.7	1.6	9.9
			(Total N)						0.3	1.8	8.2
			(Weight)						0.5	1.6	8.9
			(Juv.)		Fall				2.5	1.8	8.3
			(Adult M)						1.3	1.7	8.7
			(Adult F)						1.8	0.7	8.2
			(Total N)						0.5	2.1	7.5
			(Weight)						0.9	2.1	7.9
Maynou (1998)	Nephrops norvegicus	Spain (Catalan Sea)	n.km^{-2}	1991	April/May	40 km	Disjunctive K	Sph	4.23[5]	1.7[6]	6.5 km
Freire et al. (1992)	Munida intermedia	Spain (Galicia)	n.h^{-1}	1983	September	60 km	Point K	Sph	410.5	-	-
				1984	May			Sph	0	34	22 km
				1984	August/September			Sph	8.1	-	-
	Munida sarsi			1983	September			Sph	0	650	15 km
				1984	May			Sph	0	6300	15 km
				1984	August/September			Sph	0	83500	20 km
González-Gurriarán et al. (1993)	Liocarcinus depurator	Spain (Galicia)	n.h^{-1}	1983	September	100 km	Point K	Sph	36.1	-	-
				1984	May			Sph	90.3	-	-
				1984	August/September			Sph	0	29100	22
	Macropipus tuberculatus			1983				Sph	0	11	18 km
				1984				Sph	0	8.8	11 km
				1984				Sph	5	41	28 km

(Table IV-2 cont.)

Reference	Species	Area	Variable	Year	Season/month	Variogram max distance	Kriging type	covariance model	Nugget	Sill	Range
	Polybius henslowii			1983				Sph	80000	1750000	12 km
				1984				Sph	0	270	7.5 km
				1984				Sph	50	25000	28 km
								Shp	0		
Freire *et al.* (1991c)	*Plesionika heterocarpus*	Spain (Galician coast)	n.h^{-1}	1983	September	120 km	Point K	Sph	0	150	30 km
				1984	May			Sph	0	22500	7 km
				1984	August/September			Sph	0	215000	18 km
	Solenocera membrana-cea			1983				Sph	500	7900	15 km
				1984				Sph	20000	16000	25 km
				1984				Sph	24306	-	-
Freire *et al.* (1993)	*Liocarcinus depurator*	Spain (Galicia: Ria de Ferrol)	n.haul^{-1}	1990	September/October	8 km	Point K	Sph	3	12	3 km
	Liocarcinus arcuatus							Sph.	10	80	3.5
	Liocarcinus corrugatus							Sph.	0.8	2.2	2.3
Reference	Species	Area	Variable	Year	Season	Variogram max distance	Kriging type	covariance model	Nugget	Sill	Range
	Inachus dorsettensis							Sph.	0	30	2
	Polybius henslowii							Lin.	1800	-	-
Ungaro *et al.* (1999b)	*Liocarcinus depurator*	Italy (Adriactic Sea)	n.h^{-1} g.h^{-1}	1991/95	Spring Autumn	2^0	OK (?)	Exp.	0	10	0.48 °
								Exp.	0	27	0.21 °
	Macropipus tuberculatus			1991/95			OK (?)	Exp.	0	26	0.17 °
								Exp.	0	20	0.36 °
Simard *et al.* (1992)	*Pandalus borealis*	Canada (Laurentian channel)					Point K	Sph	-	-	-

*spring/fall; Juv: juvenile; M: males; F: females; N: number; Vario: Variogram; OK: ordinary kriging; K: kriging; Exp:exponential; Sph:spherical;

In the same work, the spatial analysis of diversity Index (H'), which shows the species diversity patterns throughout the space, showed greater diversity in fall than in spring for most sectors (Maynou *et al.*, 1996; Maynou *et al.*, 1993). Although the species were patchily distributed, the overlapped areas were associated with observed maximum diversity (Maynou *et al.*, 1996; Maynou *et al.*, 1993). Low diversity areas were associated with the dominance of certain species (Maynou *et al.*, 1996; Maynou *et al.*, 1993).

A detailed study of the distribution of *Nephrops norvergicus* (Norway lobster) off Barcelona (Conan *et al.*, 1994a; Maynou *et al.*, 1998) examined both abundance and biomass density distributions for juvenile and adult males and females in spring and autumn. Remarkably, no spatial overlap in distributions could be identified between any category and the patch size was estimated as about 7 km (raging from 6-10 km). Conan *et al.* (1988a) did, however, identify differences in distribution of adult and juvenile male and female snow crabs in Canada, again visually. Fariña *et al.* (1992) estimated the patch size of the Norway lobster on the Atlantic coast of Spain (Galicia) to be around 100 km, more than ten times greater than the patch size estimated by Maynou *et al.* (1998) for the Mediterranean. Maynou *et al.* (1998) noted that the patch size observed in the Mediterranean was smaller than the distance between samples in the Atlantic survey and hence the sampling resolution was much greater in the Mediterranean survey.

Lembo *et al.* (2000, 1999) surveyed the distribution of *Parapenaeus longirostris* and *Aristeus antennatus,* in the Tyrrhenian Sea (Italy) using stratified random otter trawls. In 1997, the *Parapenaeus longirostris* patch size (range) was 11 km while that determined from cross variogram was 31 km (using depth as a second variable), showing that patch size should be greater than 10 km. Furthermore, the use of depth as a second variable allowed a density estimation closer to the known pattern for this species, overcoming the incongruences observed by ordinary kriging. Considering the previous year abundance as a second variable, the range was kept approximately constant. These analyses were able to detect three sub-areas with higher densities within the sampling area, which persisted in the same localities from 1995 to 1997 (Lembo *et al.*, 1999). The procedure significantly increased the fit of the models. With *Aristeus antennatus* the authors also analysed the variable "percentage of females larger than median length" and in *Parapenaeus longirostris* the "number of recruits per km^2" with disjunctive kriging technique (Lembo *et al.*, 2000a; Lembo *et al.*, 2000b).

A case of stationary assumption violation in kriging was studied with *Pandalus borealis* (northern shrimp) biomass (Simard *et al.*, 1992). These authors tested several approaches to overcome the lack of stationarity. Logarithmic transformation in this case was considered inappropriate (the box-cox procedure estimated a lambda of 0.3). These authors found that the

division of the global sampled region into two homogeneous strata and kriging within each area gave the best results and overcame the lack of stationarity. Cross validation tests showed that kriging estimates were always better when interpolating very local neighbourhoods using a small number of points, so that a stratification procedure produced better estimates than the whole region approach (Simard *et al.*, 1992).

V. Effect of common geostatistical options in estimated kriging maps: a case study with *Liocarcinus depurator* (Crustacea: Brachyura) trawl survey data

V-1. PREFACE

The current chapter aims to illustrate how the selection of different options throughout a geostatistical analysis is reflected in the results obtained both in the estimates and in the maps produced. Several decisions are made during the analysis with numerous options available. Most of these options have been widely discussed but a consensus has never been reached on the best optimal approach.

Most geostatistical studies have used slightly different methods, which often makes very difficult the comparison between results. Generally, methodological options have been considered to cause minor differences in the final results but such has only been shown for well behaved data. When the data are skewed, with a relatively low number of samples (e.g. <150) and not normal distributed the application of geostatistics is probably at the limits of its applicability. For such data sets, differences due to optional choices can be unpredictable and may differ considerably from the examples performed using well-conditioned data. Most fisheries data sets, i.e. biological populations, tend to have skewed distributions, which are decidedly not normal and often under-sampled.

Here, a more 'typical' biological example, the distribution of the crab *Liocarcinus depurator* along the Mediterranean coast of Spain is analysed using geostatistical techniques. The effect of differences in method is investigated in relation to *L. depurator* distribution rather than the vicissitudes of the mathematics.

It is not the aim of the current chapter to determine the most appropriate method for general application, but to provide a basis for comparing results produced with different approaches. There are few absolute rules in geostatistics and each case should be treated as special and analysed on its merits.

V-2. ABSTRACT

The application of geostatistical methods to animal densities derived from trawl surveys is becoming more popular. Sample data are often sparse, highly skewed and quite unlike the simulated data examples used to investigate the adequacy of options available for variogram

fitting and kriging. The data from a trawl by-catch survey of *Liocarcinus depurator* were analysed using two major approaches: (a) removal of outliers and (b) logarithmic transformation of the densities. Within each approach a range of minor variations on the estimation of the spatial structure (variogram) and density were compared through kriging.

The results indicated that log-transformation produced the least robust and most unrealistic assessment of *L. depurator* spatial distribution. Removing outliers gave consistent estimates, regardless of small changes in methodology except when inappropriate spatial models were applied (exponential and Gaussian models did not fit the variogram well). Differences in the number of lags used to build the variogram or the numbers of outliers removed from the data had more effect on the spatial model parameters than did most of the procedural alterations.

Density estimates from kriging highlighted the difference between the two approaches. For example, estimated standard deviations of density were most unrealistic from the log transformation approach but were roughly half that of the original sample when the spatial model was performed with data without outliers.

In general, the failure of the methods to reflect the original sample were related to the assumptions underlying the methods. Thus the log transformation approach produces a peculiar distribution of densities, with zero densities creating considerable departure from log-normality. The resulting parameter and density estimates were thus erratic and unrealistic. Removal of outliers helped uncover the spatial structure in the crab population and led to very realistic parameter and density estimates. However, the lack of symmetry in the distribution led to unrealistic (negative) minimum density estimates when kriging forced a symmetrical distribution on the data.

Liocarcinus depurator populations along the Spanish coast were fond to show high spatial dependency with densities aggregated in patches. Patch sizes were estimated to have diameters of around 20 km. Density decreases with depth and this was adequately represented by the 'removal of outlier approach'.

V-3. INTRODUCTION

Most previous applications of spatial inference in fisheries research were performed in the context of estimating population density (abundance) or biomass rather than testing hypotheses concerning the effects of experimental treatments. The application of geostatistical analysis, in the fisheries context, has been conducted mainly for fish species (e.g. fish schools: Bahri & Freon, 2000; *Scomber scombrus* and *Trachurus trachurus*: Bez & Rivoirard, 2001;

Micromesistius poutassou: Carrera *et al.*, 2001; fish larvae: Rudstam *et al.*, 2002). The use of geostatistics for crustacean populations is less common but increasingly popularity (*Munida intermedia* and *M. sarsi*: Freire *et al.*, 1992; *Liocarcinus depurator, Macropipus tuberculatus* and *Polybius henslowii*: González-Gurriarán *et al.*, 1993; *Pandalus borealis*: Kingsley *et al.*, 2002; *Pandalus borealis*: Simard *et al.*, 1992). A general problem with results comparisons, has been the lack of quantification of the effect, if any, of methodological differences between analyses.

The analysis, geostatistical or otherwise, of trawl survey data is often hampered by low numbers of trawls relative to the area surveyed, highly skewed distributions of species densities and inevitable 'outliers' resultant from environmental heterogeneity (Maravelias *et al.*, 1996; Rivoirard *et al.*, 2000). Differences in data quality limit the reliability of any analysis. In geostatistical analysis such differences can critically influence the reliability of the variogram (Cressie, 1991), the central element of the analysis.

Although approximate normality is not a basic requirement in geostatistical analysis, the structure of the spatial distribution is more difficult to model in skewed distributions or in the presence of outliers (Cressie, 1991). Using highly-skewed simulated data, Rivoirard *et al.* (2000) have shown that the log-transformation can help uncover otherwise hidden spatial autocorrelation. However, our current observations and those of Webster and Oliver (1992) show the limitations of a simple log transformation when the sample distributions are not strictly log-normal.

Several different approaches have been suggested for improving poor variogram estimation resultant from outlying density estimates or asymmetric data distributions. Webster and Oliver (2001) suggested that outliers can be handled by performing the variogram estimation both with and without the inclusion of the outlying points. Comparison of the two variograms should indicate to the experienced analyst whether or not to include the outliers in further analysis. If the skewed distribution was caused by a few outlying points, then these could be safely excluded and further analysis conducted without transformation (Webster & Oliver, 2001). If the skewness was attributable to the underlying density distribution (e.g. truly log-normal) the inclusion of outliers and data transformation would be more applicable.

For log-normal density distributions (clumped, over-dispersed), the variogram of the log-densities should benefit in estimation from the improved symmetry over that of the sample densities (Rivoirard *et al.*, 2000). However, the penalty for transformation is that, inference from the transformed scale is only approximate in the original scale. Thus, the mean in the logarithmic scale is the 'geometric' mean in the arithmetic scale and symmetric variances in the logarithmic scale are asymmetric in the arithmetic scale. Direct comparisons between

transformed and original scales are thus difficult, even with specific adjustment prior to back-transformation (Snedecor & Cochran, 1989). In geostatistical analyses, techniques for potentially appropriate back-transformation are available both through the variogram model (Guiblin *et al.*, 1995; Rivoirard *et al.*, 2000) or through, for example, log-normal kriging at the interpolation stage (Cressie, 1991; Webster & Oliver, 2001).

Both approaches (transformation and removal of outlying points to improve symmetry) lead to problems of interpretation. Hence, log-normal kriging may give unrealistic results when the density distribution is not log-normal (Webster & Oliver, 2001). Similarly, unexplained outlying points are a 'fact of life' in biological sampling and should be considered as an integral facet of an organism's distribution when no apparent reason (e.g. transcription error) can be found to ignore them.

The objective of the current work is to analyse the effect of several alternative approaches to the analysis of a particularly problematic set of crab density measurements that could be considered fairly typical of most bottom trawl fisheries surveys. Thus, the following are considered:

(1) classic versus robust variogram estimators

(2) spherical, exponential and gaussian spatial covariance models

(3) least squares (OLS and WLS) versus maximum likelihood (ML and REML) methods of fitting the variogram.

(4) Depth as a covariate (either linear or quadratic) in the variogram and kriging interpolation (universal kriging or kriging with external trend).

In each case the 'outliers removed' and 'logarithmic transformation' approaches were also compared. The ultimate aim of the analysis was to produce guidelines for assessing the robustness of the resulting density interpolations (in the form of isodensity maps) to departures from underlying assumptions, uncertainty in the model specification and stochastic variability.

V-4. METHODS

The data consisted of densities of the portunid crab, *Liocarcinus depurator*, sampled along the Mediterranean coast of Spain, in Spring 1996. The crabs were sampled as a 'by catch' within the MEDITS project, that aimed to assess the numeric and biomass densities of fisheries resources throughout the Mediterranean Sea. The surveys were conducted by bottom trawl from 25 to 800 m deep and full details can be found in Bertrand *et al.* (2002)(see section II). Figure

II-5 shows the location of the study area and the sample positions (note that only the 1996 data set was used).

Table V-1 Summary of the options studied. Note that the main differences are highlighted in bold.

	Data	Spatial model	Variogram estimator	Fitting method	Trend	model code
(2)	Remove outliers	sph	Classical	WLS	-	Out.sph.cla.wls
	"	"	Modulus	"	-	Out.sph.mod.wls
	Log	sph	Classical	"	-	log.sph.cla.wls
	"	"	Modulus	"	-	log.sph.mod.wls
(3)	Remove outliers	sph	Classical	WLS	-	Out.sph.cla.wls
	"	exp	"	"	-	Out.exp.cla.wls
	"	gau	"	"	-	Out.gau.cla.wls
	Log	sph	"	"	-	log.sph.cla.wls
		exp	"	"	-	log.exp.cla.wls
		gau	"	"	-	log.gau.cla.wls
(4)	Remove outliers	sph	Classical	WLS	-	Out.sph.cla.wls
	"	sph	"	OLS	-	Out.sph.cla.ols
		"	"	ML	-	Out.sph.cla.ml
		"	"	REML	-	Out.sph.cla.reml
	Log	sph	"	WLS	-	log.sph.cla.wls
	"	sph	"	OLS	-	log.sph.cla.ols
		"	"	ML	-	log.sph.cla.ml
		"	"	REML	-	log.sph.cla.reml
(5)	Remove outliers	sph	Classical	WLS	-	Out.sph.cla.wls
	"	"	"	"	Linear depth	Out.sph.cla.wls.d1
		"	"	"	Quad. depth	Out.sph.cla.wls.d2
	Log	sph	"	"	-	log.sph.cla.wls
		"	"	"	Linear depth	log.sph.cla.wls.d1
		"	"	"	Quad. depth	log.sph.cla.wls.d2
(6)	Remove outliers	sph	Classical	WLS	-	Out.sph.cla.wls
	Log	sph	"	"	-	log.sph.cla.wls
	Back-transformed variogram	"	"	"	-	Blog.sph.cla.wls

Sph: spherical model; exp: exponential model; gau: Gaussian model; cla: classical estimator; mod: modulus estimator; WLS: weighted least squares; OLS: ordinary least squares; ML: maximum likelihood; REML: relative maximum likelihood. A: backtransform the model (Guiblin *et al*. 1995) and do ordinary kriging.

The relationship of crab density with latitude ('Northing'), longitude ('Easting') and depth, was initially explored by correlation analysis and scatter plots. The densities were tested for normality using Shapiro's method and a Box-Cox procedure used to determine the best normalising transformation (Sokal & Rohlf, 1994). The maximum distance in the variograms was 150 km, which corresponds to an average width of the coast established, to avoid the interference of farthest values.

The tools employed in each estimation are shown in Table V-1. Initially, a 'standard' variogram model approach was adopted (classic variogram, using a spherical model fit by weighted least squares (WLS)), both for outlying densities removed and for logarithmic transformation of all the densities. Specific changes in the methods adopted were then introduced:

(1) Using a different numbers of lags (bins or classes) in the variogram, fitting a spherical model, with WLS to the classical variogram

(2) Using the robust estimators of the experimental variogram (bin averages versus medians), for the spherical model fitted by WLS.

(3) Using exponential and gaussian models fitted by WLS, to the classic variogram.

(4) Using OLS, ML and REML, to fit the spherical model to the classic variogram.

(5) Using an external trend (depth), linear and quadratic, for fitting the spherical model to the classical variogram.

(6) Using back-transformation of the variogram (only in logarithmic transformed data), for fitting the spherical model to the classical variogram.

For all of the above, contouring of densities was done using ordinary or log-normal kriging interpolation and block kriging for the estimates, except in (5) where universal kriging with depth as either a linear or quadratic covariate was used.

Where appropriate, analysis was performed for a comparison between removing outliers and log transforming the densities. When transformation was used, log-normal kriging rather then ordinary kriging was used.

V- 4.1. Description of the methods

In a geostatistical analysis the spatial distribution of an organism's abundance is represented by an empirical variogram. The variogram shows the function which relates the distance separating pairs of points to the average (or median) variance (or semi-variance) of pairs which are separated by a given distance.

There are several formulae for estimating the variogram and in the current study, the classical and the robust estimators supplied by Cressie (1991) and Cressie and Hawkins (1980) 'respectively' were used. The robust variogram is potentially more resistant to distortion by outlying points, since the median rather than the mean in each bin is used as the estimator (Diggle et al., 2003).

Back-transformation of the variogram (as a particular option studied in the 'log data', see above), was calculated following Guiblin et al. (1995). Given a density, Z, and the transformation $L=\ln(1+Z)$, the back-transformation formula is:

$$\hat{\gamma}(h) = \left[\text{mean}(Z)^2 + \text{var}(Z)\right]\left[1 - e^{-\frac{\sigma^2\gamma_L(h)}{\text{var}(L)}}\right] \quad with \quad \sigma^2 = \ln\left[\frac{1 + \text{var}(Z)}{\text{mean}(Z)^2}\right] \qquad \text{eq. 2}$$

Where $\hat{\gamma}(h)$ is the semivariance of the back-transformed variogram and $\gamma_L(h)$ is the semivariance of the logarithmic transformed variogram.

Having obtained the empirical variogram, the crucial step is fitting an appropriate relationship between the average (or median) variances and the distance between sample pairs, i.e. the spatial covariance model. The choice of model is often done by visual inspection of the variogram, by applying some objective criteria for goodness of fit (e.g. gof, minimising functions) or by previous knowledge of the 'target species' (Rivoirard et al., 2000). Most fisheries applications have used only three models routinely: the spherical, exponential and Gaussian (for details see: Cressie, 1991; Rivoirard et al., 2000; Wackernagel, 1998).

Fitting may be done by eye and reasonable estimates of the parameters are obtained. To reduce subjectivity, however, standard curve fitting techniques are considered preferable (Rivoirard et al., 2000). To fit models to the variograms of the crab abundances, both Least Squares (Ordinary L.S. and Weighted L.S.) and maximum likelihood methods (ML and REML) were applied. Least squares methods are based on finding a model that minimises the sum of squares of the differences between the experimental variogram and the model. The commonest method used in previous works, is the weighted least squares (Webster & Oliver, 2001) whereby:

$$\sum_h w_h \left[\gamma(h) - \hat{\gamma}(h)\right]^2 \qquad \text{eq. 3}$$

is minimised. w_h is a weight applied to the sum of squares, which in the current case equals the number of pairs of abundances used to derive the individual mean (or median) estimates of the variogram.

Maximum likelihood-based methods do not require the computation of an empirical variogram and in the current study both maximum likelihood (ML) and the restricted maximum likelihood method (REML) (Cressie, 1991; Diggle et al., 2003) were employed. The maximum likelihood estimation procedures are very sensitive to departures from normality in the sample data (Cressie, 1991). The bias of the results using the ML estimator is considered to be larger than when the REML estimator is used (Cressie, 1991; Diggle et al., 2003).

According to the model fitted, the 'actual range' has to be calculated from the model range, for further comparisons. For the Gaussian model, 'actual' range = model range×√3 and for the exponential model, 'actual' model range=range×3 (Cressie, 1991). The spherical model estimates the 'actual' range.

Variogram adequacy is also dependent on the spatial resolution or distance separations (lags, classes or bins) over which the paired variances are averaged. Deciding on the resolution (number, hence width of distance classes) is usually based on visual inspection of the sample data. Techniques such as 'nearest neighbour analysis' can assist in fixing the number of classes but the final decision is invariably subjective. Different levels of distance resolution (lags) were employed on evaluation of the spherical model fitted by WLS to the average variogram (see Table V-1).

Contour maps of *L. depurator* densities were interpolated by ordinary kriging (Deutsch & Journal, 1998) for each combination of options. Diggle *et al.* (2003) considers it as a Generalised Linear Model (McCullagh & Nelder, 1983) in a spatial context, whereas Cressie (1991) sees it as a generalisation of universal kriging to non-Gaussian data. The procedure applied to fit this method was to find a suitable transformation of the raw data to ensure normality (as explained above) and then model the autocorrelation function $\gamma(\mathbf{h})$ taking into account the explanatory variables $f(\mathbf{x})$.

Journel and Huijbergts (1978) considered that the back-transformation procedure during log-normal kriging is sensitive to departures of log-normality, hence the estimates of Z (e.g. crab's density) can be distorted. These authors suggested that in deviations from strict log-normality, the kriging estimates $p(Z^*)$ should be divided by a correction factor (Q). Q is equivalent to the estimated mean, divided by the sample mean. So, when there is no difference in the estimates due to the back-transformation, Q~1. However, under departures of strict log-normality, it is not possible to formulate a transformation to correct the distortions of the kriging variance (Journel & Huijbergts, 1978; Webster & Oliver, 2001).

To evaluate the performance of the various techniques employed, the summary statistics (range, mean, median and quartiles) of each kriging prediction were compared with the summary statistics of the sample data. When the model is appropriate, the summary statistics of the estimates should coincide with those of the sample.

The last criterion used to evaluate the models, was the kriging standard deviation (kriging error). Kriging error was computed using block kriging (when possible) and ordinary kriging, as the squared root of the mean predicted variance. A good model is expected to minimise the residual error, so the lower the mean kriging error the better the model. Ultimately, the conclusions were done based on a final visual interpretation of the density contour maps.

V-5. RESULTS

V- 5.1. Exploratory analysis

Figure V-1 a-c shows the *L. depurator* densities to be highly skewed (coefficient of skeweness=6.019). The Box-Cox procedure recommended a natural LOG transformation (λ=0.0299) to obtain an approximation to normality. Figure V-1 d-f shows that Ln(density +1) shows no significant relationship with latitude ($r^2 = 0.123$, p = 0.22) nor with longitude ($r^2 = 0.118$, p = 0.24) whereas a significant negative relationship was evident with depth ($r^2 = 0.472$, p <0.001). Thus no geographic trend was evident in the *L. depurator* population densities but crabs became increasing less abundant with depth. Further, eleven large densities were identified as extreme values, i.e. outliers, by exceeding 1.5 times inter-quartile range.

V- 5.2. Variogram analysis

Variation of the spatial model estimated according to different options

The variogram of the original crab densities showed decreasing variance with distance between samples, and hence indicated no standard spatial structure to the population (see Figure V-2 a). Both removal of the 11 outlying densities and natural log transformation produced variograms that indicated a sensible relationship between variability and sample separation distance (e.g. see Figure V-2 b and c), i.e. spatial autocorrelation. Therefore, the spatial modelling of all the methods tested was done both for data without outliers and for natural logarithm data. For brevity the remaining variograms (for all options tested) are not presented (see Table V-1 for details).

Table V-2 shows the parameters estimated, resultant from the various techniques employed to estimate the variogram or fit the spatial model to the densities with outliers removed and the natural log transformed densities. The variogram estimated through removal of outliers (classical estimator) and the spherical model fitted by WLS is used as the 'base model' for tabulating percentage differences. Although model variance (nugget and sill) estimates seem to vary widely with the technique employed that is because variances in the log scale (even if back-transformed) are not comparable in the arithmetic scale. The percentages of the total attributable to each component, however, can be directly compared. The greatest differences lay consistently between the two data sets (outliers removed or transformed). The relative nugget (unexplained variation or measurement error) varied from 0 to 15 % (median 7%)

when outliers were removed and from 28 to 52 % (median 45%) for the log-transformed densities.

Figure V-1: Bathymetric (a-b) and geographic (Easting=longitude and northing=latitude)(b-c and e-f) variation of *Liocarcinus depurator* density (crabs.km^{-2}) (a-c) and LOG transformed density (d-e) on the Spanish Mediterranean coast.

a)   b)   c)

d)   e)   f)
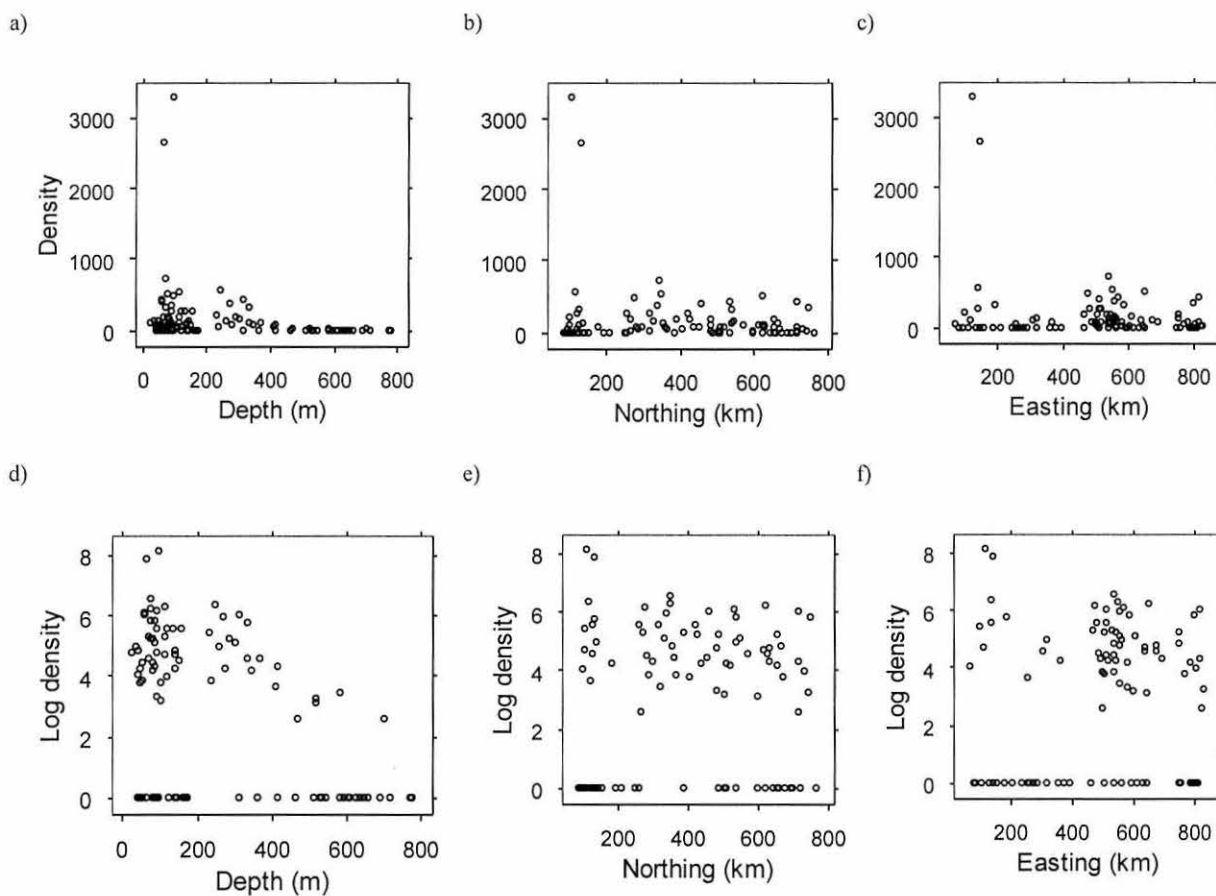
Figure V-2: Variograms of *Liocarcinus depurator* density, in the Spanish Mediterranean coast. Cases considered were all the data, LOG transformed data and data without outliers. In these last two cases the variogram model fitted is also presented.

(a) All data, no transformation   (b) Log transformed   (c) Data without 11 outliers
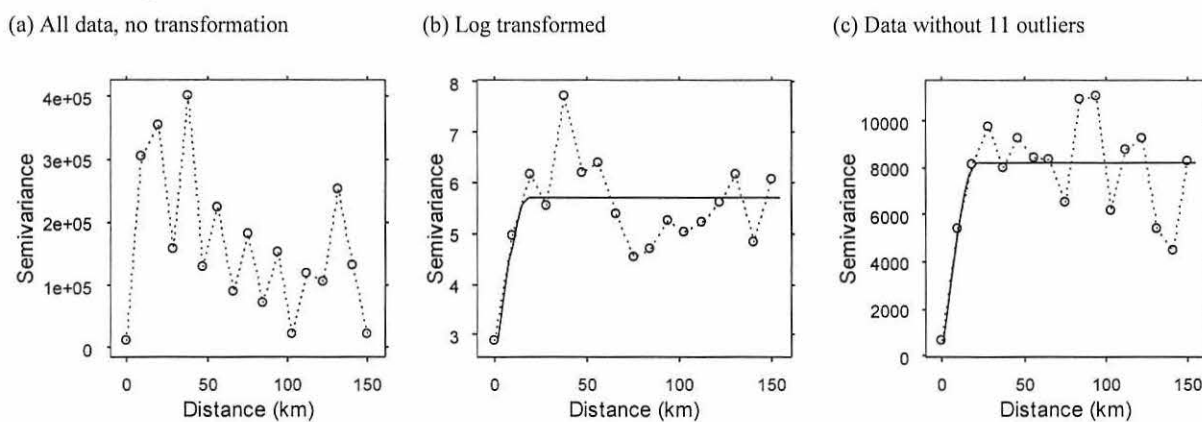
The degree of spatial dependency (estimated sill as a percentage of the total variance) ranged from 28 to 100% (Table V-2). Removal of outliers always gave much higher spatial dependencies (median=93%) than did log transformation (median=33%)(Table V-2). The variability in spatial dependency was ±11.3% (SD of deviations from the base model) for the log transformed models but nearly half that (±5.5%) when only outliers were removed. Spatial dependency was substantially improved for the log transformed abundances fitted with either a linear or quadratic covariate in depth (see Table V-2).

The range (often interpreted as patch 'size', i.e. the diameter of *L. depurator* aggregations) varied from 5 to 32 km between the 18 different methodological procedures (Table V-2). Relative to 'base model' estimate of 21 km, 12 of the estimates were within ± 5 km. Using the median, rather than the average, to estimate the variogram (i.e. modulus estimator instead of classical estimator), however, resulted in a 14% (log transformed) to 57% (removing outliers) increase in range estimate. The exponential and Gaussian models fitted to the variograms resulted in a considerable decrease in the estimated range, which was between 13 and 19 km (actual range) irrespective of transformation (which represent a decrease of about 10-38%). The fitting of a spherical model by OLS made no substantive difference to the estimated range for transformed or outlier-less densities. However, ML and REML fitting methods led to a doubling of the estimated range (relative to the 'base') for log transformed abundances while having no substantive effect when outliers were removed. In every other case, log transformation led to a smaller range estimate than that estimated without transformation (median 18 km and 21 km, respectively).

Addition of a covariate i.e. depth (or depth^2), provided the best comparability of parameter estimates between transformed and non-transformed densities. Range estimates from the transformed abundances were only 2 km less than the 'base' range and those for the outlier-less abundances equalled the 'base' range. The degree of unexplained variability (nugget) for the transformed densities was noticeably reduced with the inclusion of the covariate.

The backtransformation of the variogram model gave the worst results in terms of the spatial dependency (28%) (relative nugget, 72%), although the estimated range was similar to the logarithmic transformed data base model.

Table V-2: Summary of the estimated variogram models of *Liocarcinus depurator* density, for each method. % var. indicates spatial dependence. Actual range of exponential and gaussian model are given in parenthesis (see text for details). SpD indicates spatial dependency.

Data		Model	Nug	Sill	SpD	Dif. (%)	Range	Dif. (%)	model code
(2) Remove out-liers		Classical	540.9	7682	93		20.680		Out.sph.cla.wls
"		Modulus	618.4	3600	85	-9	33.130	60	Out.sph.mod.wls
Log		Classical	2.885	2.811	49	-47	17.081	-17	log.sph.cla.wls
"		Modulus	1.795	1.628	48	-48	23.923	16	log.sph.mod.wls
(3) Remove out-liers		sph	540.9	7682	93		20.680		Out.sph.cla.wls
"		exp	119.1	8108	99	6	6.432 (19)	-8	Out.exp.cla.wls
"		gau	578.5	7647	93	0	9.351(16)	-23	Out.gau.cla.wls
Log		sph	2.885	2.811	49	-47	17.081	-17	log.sph.cla.wls
		exp	2.679	3.011	53	-43	4.692 (14)	-32	log.exp.cla.wls
		gau	2.804	2.891	51	-45	7.786 (13)	-37	log.gau.cla.wls
(4) Remove out-liers		WLS	540.9	7682	93		20.680		Out.sph.cla.wls
"		OLS	641.7	7544	92	-1	20.680	0	Out.sph.cla.ols
		ML	0	8786	100	8	18.581	-10	Out.sph.cla.ml
		REML	0	8906	100	8	18.855	-9	Out.sph.cla.reml
Log		WLS	2.885	2.811	49	-47	17.081	-17	log.sph.cla.wls
"		OLS	2.058	2.318	53	-43	16.308	-21	log.sph.cla.ols
		ML	2.179	2.712	55	-41	40.488	96	log.sph.cla.ml
		REML	2.169	2.812	56	-40	41.678	102	log.sph.cla.reml
(5) Remove out-liers		-	540.9	7682	93		20.680		Out.sph.cla.wls
		Linear depth	0	7499	100	8	20.660	0	Out.sph.cla.wls.d1
		Quad. depth	0	7093	100	8	21.390	3	Out.sph.cla.wls.d2
Log		-	2.885	2.811	49	-47	17.081	-17	log.sph.cla.wls
		Linear depth	0.901	2.109	70	-25	18.869	-9	log.sph.cla.wls.d1
		Quad. depth	0.794	2.068	72	-23	19.158	-7	log.sph.cla.wls.d2
(6) Remove out-liers			540.9	7682	93		20.680		Out.sph.cla.wls
Log			2.885	2.811	49	-47	17.081	-17	log.sph.cla.wls
Back-transformed variogram			128494	49297	28	-70	14.850	-28	Blog.sph.cla.wls

Changing in the number of lags

Table V-3 shows the relationship between the estimated parameters from the 'base' model and the number of lags (distance classes) used to construct the variogram. 10 lags represents distance classes about 15 km wide and 25 lags, classes about 6 km wide, for averaging paired abundance differences within the 150 km sections of coastline. The sill represents spatial dependency (variation explained by the spatial model) when expressed relative to the nugget (unexplained variation). The value of the nugget is directly and negatively correlated to that of the sill. For the most part, sill values for lags greater than 11 and less than 22 are fairly constant giving a spatial dependence prediction of 93-96% (Table V-3). The sill steadily decreases for lags of 22 or more (>6.8 km) to a low of 79% of the total variability.

Table V-3: Spatial models obtained from WLS estimation of variograms made with different number of lags (bins), using the same data set (method: Out.sph.cla.wls)

N° of lags	Nugget	Sill	% nugget	% variance	Range	Min. fun (×10⁻⁹)
10	5475.3	2719	66.8	33.2	27.55	1.189
11	5197.9	3029	63.2	36.8	31.29	4.025
13	592.7	7637	7.2	92.8	17.48	3.512
14	592.7	7694	7.2	92.8	22.01	2.599
15	626.9	7601	7.6	92.4	21.48	3.133
16	345.1	7886	4.2	95.8	21.00	3.312
17	540.9	7682	7.0	93	20.68	3.00
18	1417.6	6807	17.2	82.8	20.57	6.010
19	335.0	7877	4.1	95.9	17.31	3.822
20	329.3	7872	4.0	96.0	16.31	5.440
21	582.3	7638	7.1	92.9	19.89	4.167
22	1254.8	6944	15.3	84.7	22.57	5.998
23	1221.6	6976	14.9	85.1	22.56	5.714
24	1511.2	6697	18.4	81.6	24.37	5.335
25	1761.3	6420	21.5	78.5	22.99	5.882

Presumably, greater small-scale heterogeneity is increasing the nugget, as distance class intervals become smaller. For lags of 10 and 11 the nugget exceeds the sill and the spatial model explains only 33-34% of the variability. Apart from the two high sill estimates provided by lags of 10 and 11 (equivalent to low sill values), 10 of the remaining 13 estimates between 20 and 24 km. Excluding the two high estimates, the average range is 21 ± 2.5 km. In general, the variation in sill and range estimates for lags in excess of 11 appears to be as great if not greater than that induced through different fitting methodologies (see Table V-3).

Effect of the outliers removed

The effect of differing numbers of outliers removed from the variogram base model estimation is shown in Table V-4. Remarkably, the removal of between three and 13 (2.2 – 9.5% of the total number of points) "outliers" has a considerable impact on the model parameters. Pre-

dictably, the residual sum of squares increases as fewer outliers are removed. Generally, higher spatial dependencies are shown when more outliers are removed but the lowest spatial dependency (22%) was observed when seven outliers were removed. The range estimates vary from 16 – 30 km, both extremes associated with sill values <5400. The three higher sill estimates (spatial dependencies from 49 – 95%) were all accompanied by range estimates of around 20 km. However, the variation of lags in relation to the number of outliers removed may have a string effect in the estimates.

Table V-4: Parameters of the models computed when a different criterion for the outliers removed is used. Standard methods, consider as an outlier 1.5 times interquartile range values. Values removed indicate how many values were removed from the sample data, according to the criterion used: e.g. when it is considered as an outlier 1.5 times the inter-quartile range, ten values were considered an outlier and so were removed from the sample data. Greater than 3 times the interquartile range was not possible to compute because the spatial structure was not found within the variogram.

× inter-quartile range	values removed	% removed	Nugget	Sill	% nugget	% var	Range	Min. fun.10^{-9}
1	13	12.4	648.5	5352	10.8	89.2	15.97	1.20
1.5	11	9.5	405.2	7818	4.9	95.1	20.5	3.02
2	7	6.7	8903.6	2593	77.4	22.6	30.17	5.28
2.5	4	3.8	5711	10618	35.0	65.0	20.27	9.18
3	3	2.9	9450.4	9237	50.6	49.4	19.05	9.65

There is a lack of a consistent pattern to parameter estimates when (a) very few points in total are removed and (b) the outlying points in the 2.5 inter-quartile range bracket (4 points) must include the three points previously tested in the 3.0 inter-quartile range bracket. The fact that removal of one more point causes a 15% difference in explained spatial dependence must cause some concern. Furthermore, the removal of an additional three outliers (2.0 interquartile range bracket) causes a sensible decrease in the residual semi-variance but is accompanied by a 42% decrease in relative sill and a 50% increase in range. Such, apparently random and large fluctuations in parameters from little material change in the data require further investigation.

V- 5.3. Kriging results

Table V-5 shows mean and range *L. depurator* densities, estimated by kriging, for each methodological procedure. For every procedure, the estimated means in the removal of outliers data lay within 11% of the base model and most are very close to the mean of the sample data (including outliers = 161 crabs.km^{-2}). However, every log transformation procedure overestimated the base model mean density by between 59% and 182% except when the robust esti-

mator was used in the experimental variogram calculation. Back transformation of any sort, results in differences from the original scale means, but log back transformation normally provides lower mean estimates (the so called geometric mean). For that reason Journel & Huijbergts (1978), contoured log transformed estimates after standardising the estimates to have the same mean as the sample data.

Estimated minimum densities in the data with outliers removed, were negative (i.e. unreal) in all but the exponential model procedure (the model is constrained to zero). The variation in minimum estimate was up to a 3.8 fold difference from the base model estimate of -53 crabs.km^{-2}. Minima for the log transformed approach were obviously positive ranging from 1 to 2.6 times greater than the base model estimate. The base line maximum density was consistently underestimated by the log transformed densities, ranging from 441 – 1239 crabs.km^{-2} while those for the outlier-less densities lay within ±20% of the base line estimate. For both approaches the range in maximum estimate was very similar at around 770 crabs.km^{-2}. Estimated mean standard deviations were fairly consistent between procedures for densities with outliers removed (a range of 31 crabs.km^{-2}) but extremely variable (range of 9399 crabs.km^{-2}) and ludicrously high for the log transformation approach.

In general, kriging density estimates for samples having outliers removed were more self consistent and less sensitive to changes in the procedure than were the log transformed samples. In addition, all density and error estimates based on the log transformed data generally gave completely unrealistic approximations to the known sample distribution. The approach of removing outliers provided completely unrealistic estimates of the minimum densities and consistently underestimated the sample standard deviation by a factor of two.

The technique of 'Block Kriging' was also used to estimate population density parameters in relation to the procedures applied to the sample densities with outliers removed, according to (Maynou, 1998). The results did not differ substantially. In each case the block kriging mean density estimate was between 0.4 to 0.6% lower than mean density estimated by ordinary kriging. Estimated standard deviation were also consistently lower (between 15 and 26%, average 20%). The result is as one would expect, since the technique uses 'within block' semi-variances hence averages out some of the variability. The nugget variance was zero for both maximum likelihood methods of fitting the spherical model (see Table V-2) yet the reduction in standard deviation estimates for these by block kriging was not substantially smaller than for other procedures. Although there is a significant, but not necessarily linear, correlation between estimated standard deviation (ordinary kriging) and nugget ($r = -0.863$, DF = 5, $p = 0.012$), the percentage difference between block kriging and ordinary kriging

standard deviation shows no significant correlation with the nugget ($r = 0.112$, $DF = 5$, $p = 0.811$).

Table V-5: Summary of the ordinary kriging (O.K.) and block kriging (B.K.) estimates with mean error (kriging standard deviation of the estimates) of *Liocarcinus depurator* density, for each method. See specifications of the methods in Table V-1. CV (standard deviation/mean).

Data	Spatial model	O.K. Density Min	O.K. Density Max	O.K. Density Mean	O.K. Error Mean	O.K. C.V.	B.K. C.V.	model code
Raw data	-	0.0	3279.0	161.0	153.0	1.0		
(2) Remove outliers	Classical	-56.3	1907.3	161.6	83.4	0.5	0.4	Out.sph.cla.wls
"	Modulus	-171.4	1768.6	147.6	55.9	0.4	0.3	Out.sph.mod.wls
Log	Classical	18.7	1320.0	347.6	6036.8	17.3		log.sph.cla.wls
"	Modulus	88.3	632.0	161.7	421.8	2.6		log.sph.mod.wls
(3) Remove outliers	sph	-56.3	1907.3	161.6	83.4	0.5	0.4	Out.sph.cla.wls
"	exp	6.6	1531.0	156.4	86.5	0.6	0.4	Out.exp.cla.wls
"	gau	-266.8	2287.1	160.0	81.8	0.5	0.4	Out.gau.cla.wls
Log	sph	18.7	1320.0	347.6	6036.8	17.3		log.sph.cla.wls
	exp	28.1	953.4	348.3	6126.2	17.5		log.exp.cla.wls
	gau	12.2	1561.2	348.2	5980.4	17.1		log.gau.cla.wls
(4) Remove outliers	WLS	-56.3	1907.3	161.6	83.4	0.5	0.4	Out.sph.cla.wls
"	OLS	-53.0	1874.8	161.5	83.4	0.5	0.4	Out.sph.cla.ols
	ML	-116.5	1982.4	160.9	86.6	0.5	0.4	Out.sph.cla.ml
	REML	-107.8	1984.5	161.1	86.9	0.5	0.4	Out.sph.cla.reml
Log	WLS	18.7	1320.0	347.6	6036.8	17.3		log.sph.cla.wls
"	OLS	19.1	1267.9	340.8	5808.2	17.0		log.sph.cla.ols
	ML	14.4	2962.7	431.5	8913.3	20.6		log.sph.cla.ml
	REML	14.8	3490.5	453.7	9821.1	21.6		log.sph.cla.reml
(5) Remove outliers	-	-56.3	1907.3	161.6	83.4	0.5		Out.sph.cla.wls
	Linear depth	-231.9	2118.7	143.5	78.4	0.2		Out.sph.cla.wls.d1
	Quad. depth	-115.3	2165.5	162.9	78.1	0.2		Out.sph.cla.wls.d2
Log	-	18.7	1320.0	347.6	6036.8	17.3		log.sph.cla.wls
	Linear depth	-0.9	2384.5	328.4	4175.9	12.7		log.sph.cla.wls.d1
	Quad. depth	-1.9	1488.8	257.3	2743.6	10.6		log.sph.cla.wls.d2
(6) Remove outliers		-56.3	1907.3	161.6	83.4	0.5		Out.sph.cla.wls
Log		18.7	1320.0	347.6	6036.8	17.3		log.sph.cla.wls
Back-transformed variogram		16.7	1318.0	345.6	673.2	1.9		Blog.sph.cla.wls

Figure V-3 shows contour maps of *L. depurator* abundance along the Mediterranean coast of Spain derived from ordinary kriging for each of the methodological approaches. Virtually every approach was able to identify and adequately represent patches of high crab density. Thus, the major differences for maps created with outliers removed lies between the fitted models (exponential foreshortening the range of densities and Gaussian increasing the range) in comparison to the rest. In general the log transformation approach foreshortens all

density ranges and the density distribution maps tend to resemble that for the Gaussian model fitted to densities with the outliers removed.

Figure V-3: Maps of the ordinary kriging estimates of *Liocarcinus depurator* density along the Mediterranean coast of Spain, using different methodological options. See Table V-1 for the information on the each map title and respective details. Longitude scale refers to the first left bottom graph, the remaining graphs are repetitions with the same scale. Color bar indicate density levels.
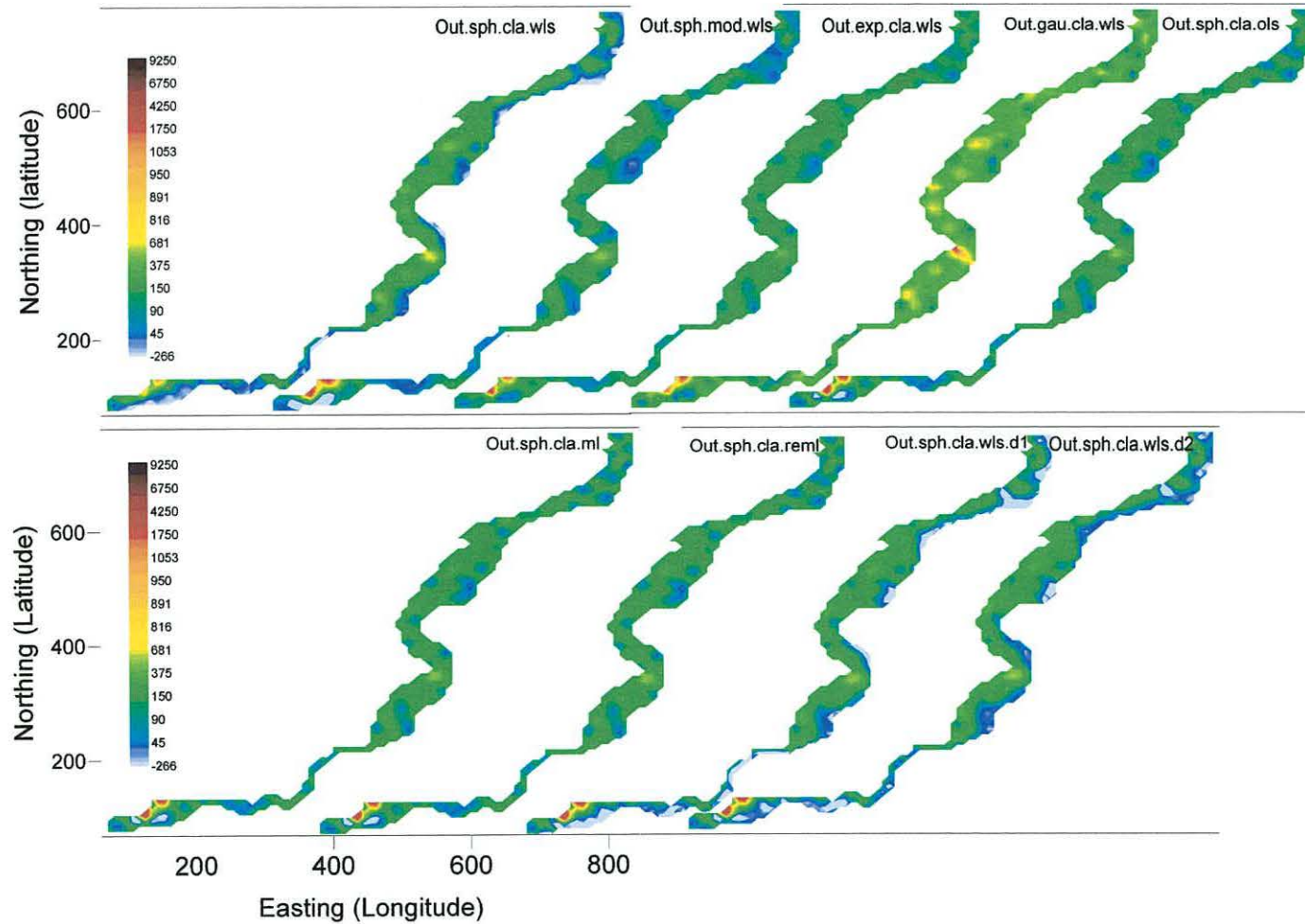
(Figure V-3 cont.)
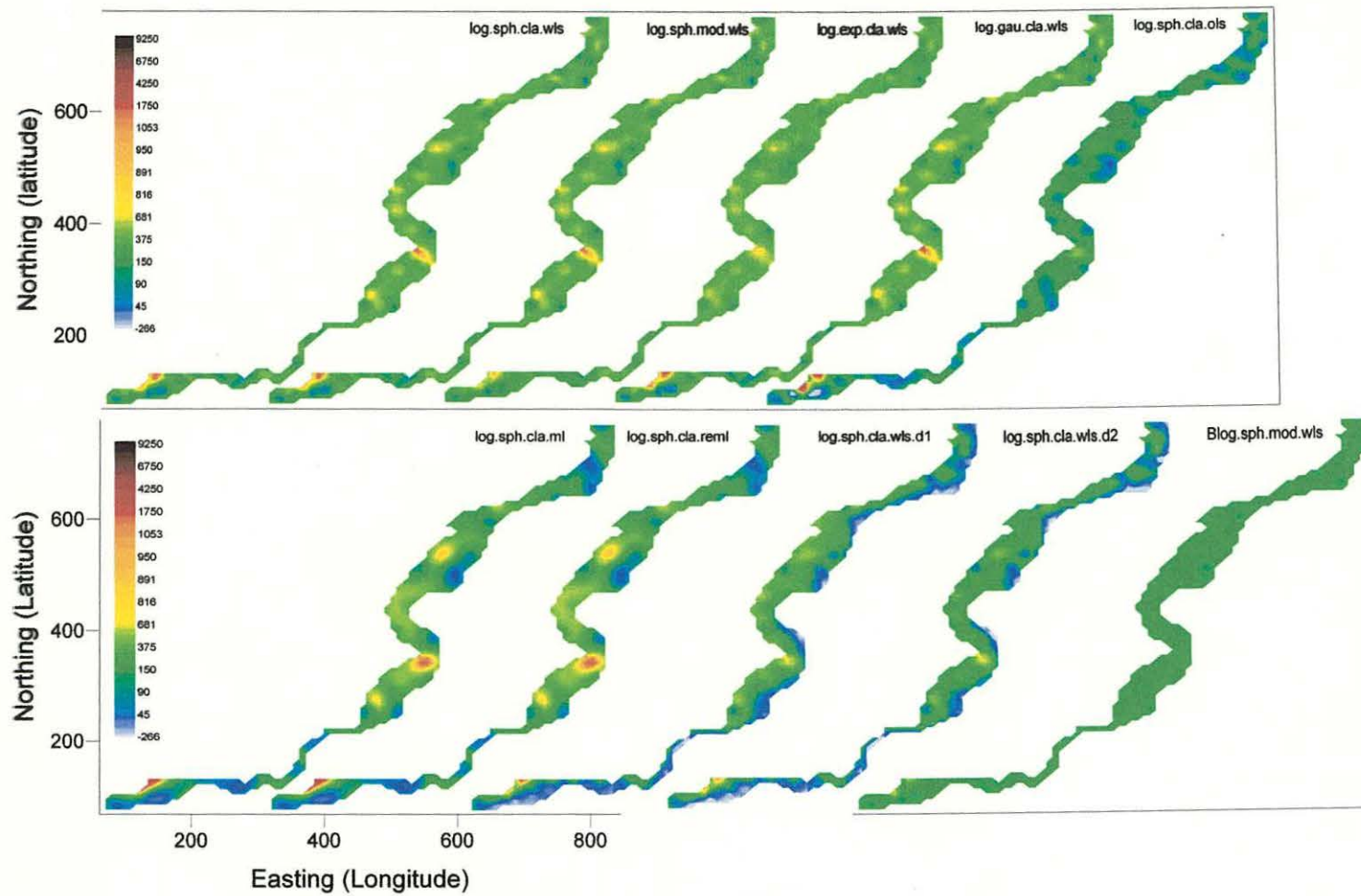
A gradient in *L. depurator* density from high abundance at the coast to lower offshore in deeper water (see Figure V-1) was particularly evident in the southern area (Alborán Sea) and in the largest area of continental shelf, near the Ebro Delta. Apart from when depth (or its square) was included as a specific covariate to induce the trend, only the base model (see Figure V-3) adequately reflected that onshore/offshore gradient.

V-6. DISCUSSION

Irrespective of methodology applied to estimate the variogram function, the approach of using log-transformed densities always resulted in substantially lower spatial dependency and more variable range estimates than the approach of removing outliers. However, within each approach, the variations in methodology generally caused little substantive differences in the model parameters except when less appropriate models (Exponential or Gaussian) were applied. The 'remove outliers' approach led to more consistent estimates throughout but, the inclusion of covariates in depth caused a considerable convergence of the two approaches.

The variation in spatial dependency for different numbers of lags between 13 and 21 had a coefficient of variation (cv) of only 4% but for all lags employed (10 - 25) the cv was 24%. The cv for spatial dependency overall methods applied to the densities with outliers removed was 6% hence much more variability was introduced by employing too many or too few lags than was introduced even by fitting inappropriate models.

Methodological changes led to considerable variability of range estimate for the log transformed estimates (cv = 39%) and very much less so for the removal of outliers (cv = 8%). In both cases use of an inappropriate model (exponential or Gaussian) led to excessively low estimates of the range (see Table V-2). Once more the variability in range estimates from using different lag numbers (cv = 18%) was more than double that obtained from different methodological procedures. Clearly, arriving at an appropriate averaging distance for the experimental variogram is more influential on the values of estimated parameters than is the choice of fitting method as long as an appropriate model has been identified.

The current data, *L. depurator* densities, provided a decidedly non-normal distribution, heavily skewed with a mode of zero (no crabs!). Logarithmic transformation did not improve the quality of the distribution since so many (41% of the 105 measurements) were zero and cannot be adequately modelled in a log scale, even by the pragmatic convention of adding 1 to each density. The spatial models examined in the transformed data were thus very variable in parameter estimate and only began to converge with the untransformed approach when covariates in depth were included. Using the untransformed data and removing obvious outliers

led to more robust parameter estimates that were only really influenced by trying to fit inappropriate models. The large number of zero densities can clearly influence the raggedness of the expected variogram asymptote and is probably reflected in the occasional large, possibly random, variation in spatial dependency seen with lag number.

The mean kriging density estimations for the log-transformed data were generally 1.5 – 3 times higher than the original sample mean. The estimates from removing outliers were remarkably similar to the sample mean, even when inappropriate models were used. Interestingly the use of a median estimator for the variogram resulted in a lower mean kriging density estimate when outliers were removed, as one would expect from a highly skewed distribution. However, the median estimator for the log transformed densities provided the closest estimate to the mean of any log procedure. The standard deviations of the kriging estimates for the log transformed approach were extremely variable and barely came close to realistic estimates, even when a covariate in depth was used. Those for the removing outliers approach were very consistent but roughly half that estimated from the original sample. Yet again the transformation approach for the *L. depurator* data can be considered inappropriate.

The major deficiency with removing outliers was in the estimation of minimum densities. In this case we know that the minimum density surveyed was zero and it is moot point as to whether such null returns aid or confuse attempts to map spatial structure in populations as opposed to simply mapping distribution. Negative densities are clearly impossible and are a result of applying symmetrical distribution techniques to heavily skewed data. The contour maps of distribution/spatial structure ultimately indicate how successful the techniques are at approximating reality.

Maps of the kriging predictions (adjusted to the sample mean for log transformed densities but not when outliers were removed) showed that removal of outliers gave more realistic results than did log transformation. The inclusion of a covariate with depth improved the clarity of the depth trend in the maps but such was still evident in the base model predictions. Although it is known that *L. depurator* abundance is a quadratic function of depth (Abelló *et al.*, 1988) little difference was found between estimates derived from depth included as a linear or a quadratic trend.

The aim of geostatistics is to build a reliable representation of the spatial structure (the absolute size of aggregations in space) of a 'population' from sample data. The objective is to then apply that knowledge to estimate density in positions not sampled within the original sample area with the aim of obtaining more realistic representations of the 'population' distribution. The ultimate result is the 'smoothing' of the more ragged sample estimates by removing much of the inherent variability in sampling technique, sampling strategy and to some

extent environmental heterogeneity within sampled areas. The work detailed above indicates that transformation of *L. depurator* densities destroys the spatial inter-relationships and the results cannot be adequately reflected in the original scale even when applying pragmatic rescaling to the original average. Removing 'outliers' from the density data not only allows the spatial structure of the 'population' to be seen but also retains the spatial inter-relationships between densities. It is clear, however, that the fundamental choices influencing the representation of spatial structure are (a) the number (and hence relative magnitude usually) of outliers to remove, (b) the resolution of the experimental semi-variogram (number of lags) and (c) the appropriateness of the mathematical model fitted to the variogram. Most other options have little influence.

It is thus recommended that 'messy' biological sample data (the usual sort) be used in its original, density scale. If no spatial structure can be observed with all the data, removal of outliers should be considered to discover if they 'hide' the spatial structure. The effect of different numbers of outliers removed on the ability of the variogram to present a spatial structure should be examined. If no spatial structure is identified then there is probably little point in searching for an adequate transformation that might just find it. Attention should also be given to the meaning of zero density: if a survey of 150 km^2 gives zero density from 49 trawls and one trawl with lots of crabs from right in the middle of the area, it is hardly worth investigating the spatial structure. Varying the number of lags in producing the variogram is essential to arriving at a sensible variogram. It seems that the effect of random combinations of differences does not give a simple relationship between parameter estimates and numbers of lags employed. The number of lags to use must lie comfortably within a 'stable' region of the parameter *vs* lag number relationship. Lastly, choice of the variogram model will have a great effect since it defines the 'spatial structure'. Several authors suggest that a pragmatic fit by eye is as good as any mathematical model (Maynou, 1998). The current results would, to some extent, support such a suggestion since neither exponential nor Gaussian models would be anyone's first choice to fit by eye to the variograms presented. With our current knowledge, geostatistics cannot be applied automatically to data (especially the type of data derived from biological sampling). Choices must be largely guided by expert knowledge of the organism's biology and the objective in applying geostatistical techniques in the first place.

VI. Geostatistical analysis of *Liocarcinus depurator* on the western Mediterranean coast of Spain, from 1994 to 2003: influence of oceanographic phenomena on crab densities

VI-1. ABSTRACT

The density of the portunid crab *Liocarcinus depurator* was analysed using non-linear geostatistical techniques. Bottom trawl estimates of abundance from 1994 to 2003, covering a depth range of 50 to 800 m, throughout the Mediterranean coast of Spain have been analysed. The variation of the spatial distribution was modelled through variogram analysis using depth as a covariate. Patch size varied from 20 to 75 km. Crab density showed a general decrease overall, from 1994 to 2003. High-density *L. depurator* patches areas were identified as either occasional or permanent (always present every year). Each high-density patch appeared to be associated with upwelling or river input. The most favourable areas for the species within the Spanish Mediterranean coast were the Ebro Delta and the Western Alborán Sea. The application of non-linear geostatistical techniques proved useful in identifying permanent population focus for *L. depurator* hence highlighting regions of special interest for conservation or species management policies.

VI-2. INTRODUCTION

The traditional approach to managing fisheries considers target species as independent, self-sustained populations. The deficiency of this approach is clear since it ignores the interactions between the rest of the ecosystem and the resource. An ecosystem approach to management, however, requires considerably more effort in identifying and monitoring the numerous interactions, which involve the resource. The spatial structure of the environment and the biological communities therein have been considered the major determinants of ecosystem 'functioning' (Legendre, 1993). Thus the study of the detailed spatial distribution of non-commercial species (such as the main fisheries by-catch) is a fundamental step towards understanding the consequences of fishing within an ecosystem and hence towards an efficient management strategy. The Mediterranean Sea is characterised by spatial heterogeneity and multi-species fisheries. Despite the ecosystem complexity, available literature focuses on species with greatest commercial value (e.g. hake). Other species received little attention or the studies were restricted to a small spatial scale.

Liocarcinus depurator is the dominant brachyuran by-catch in Mediterranean demersal fisheries, down to 200 m depth (Abelló *et al.*, 2002; Abelló *et al.*, 1988; Sardà & Palomera, 1981). Its ecological importance within the Mediterranean ecosystem has been previously well established. Highest *L. depurator* densities are found at depths of between 50-100 m in the Catalan Sea (Abelló, 1993; Abelló *et al.*, 1988), with especially high abundance in the vicinity of the Ebro and Llobregat deltas. In the south, maximum densities are found in roughly the same depth range (36 to 90 m) (García-Raso, 1984). No previous study has estimated the distribution of *L. depurator* along the whole Spanish Coast.

Species abundance distribution and hence population spatial structure has been analysed either through traditional statistics comparing mean densities between geographic locations along environmental gradients or through geostatistical examination of the underlying spatial structure of populations interpolated over the whole region sampled.

A geostatistical analysis initially characterises the way in which a 'population' is aggregated in space (the spatial structure, resultant from the interaction between the behaviour of an organism and the heterogeneity of its environment). Generally, that characterisation is used to improve the 'accuracy' of density distribution mapping procedures. However, observed changes in the spatial structure of a population are of themselves indicative of ecological change resultant from altered species behaviour or altered environmental conditions. For example, the collapse in stocks of the northern cod was accompanied by a change in the spatial structure of the population, that preceded the realisation that stocks were endangered (Hutchings, 1996; Warren, 1997).

In the present study, the distribution and density of *Liocarcinus depurator* off the Mediterranean coast of Spain between 1994 and 2003 has been examined though the use of non-linear geostatistics. A major aim is to examine the variability in spatial structure from year to year and determine whether such changes reflect long term changes in population density. No comparable study over such a long time scale or geographic area has been conducted on this species.

VI-3. MATERIAL AND METHODS

VI- 3.1. Survey details

The study area encompassed the Mediterranean coast of Spain, from Gibraltar to Cape Creus (Figure II-5). A bottom trawl survey from the RV 'Cornide de Saavedra', took place annually from 1994 to 2003, within the MEDITS research programme framework (Bertrand *et al.*,

2002). This European Union project aimed to estimate population distribution as well as demographic structure of benthic and demersal organisms on the continental shelves and their upper slopes throughout the European Mediterranean (Bertrand *et al.*, 2002). Sampling areas were distributed almost evenly along the Spanish coast and random trawls made across the depth profile in each area. The distribution of each set of trawls was a compromise between the needs of traditional statistics and those of geostatistics (in :Bertrand *et al.*, 2002; Green, 1979; Hilborn & Walters, 1992).

The GOC 73 bottom trawl (Fiorentini *et al.*, 1999), designed for experimental fishing, was used throughout. To increase the catch of demersal species it had a vertical opening slightly higher (4 m) than the most common commercial trawls used in the Mediterranean. The codend stretched mesh size was 20 mm, hence smaller than commercial mesh sizes. Hauls at depths of less than 200 m lasted 30 minutes. Deeper hauls, down to 800 m, lasted 60 minutes. All *Liocarcinus depurator* caught were counted, weighted and measured immediately after capture. Crab density was standardised to trawl swept area (number.km^{-2}).

A total of 1098 hauls were performed from 1994 to 2003 covering a total area of 45331 km^2 of the Spanish Mediterranean. Between 77 and 134 hauls were performed each year. The whole coast was well sampled except for Ibiza, which was not sampled every year and subsequently excluded from the analysis. Further, the northernmost part of North Catalonia was not sampled in 1998. The continental shelf in the Gulf of Vera and the shelf slope of the Ebro Delta area was not extensively sampled due to the narrowness of the shelf or the steepness of the slope.

Sampling took place between April and June as shown in Table II-3. The latest surveys were those of 1994 and 2000, which ended on the 19th and 23rd June, respectively, while the earliest were those of 1995 and 2003, which started on the 22nd and 24th April, respectively.

See section II, for the oceanographic characteristics of the sampled area and further details on the survey.

VI- 3.2. Geostatistical analysis

In a geostatistical analysis, the spatial interrelationship between densities is explored by computing an empirical variogram, the basic tool of geostatistics (Rivoirard *et al.*, 2000). The variogram is derived from the semi-variance of all pairs of densities measured at locations separated by increasingly distance *h*. A monotonic increase of the semi-variance with increasing distance separating the sampling locations indicates the presence of a spatial autocorrelation and hence spatial structure to the population.

In section V it was already reported a comparison of various Geostatistical techniques with part of the current data (abundances for 1996). They discovered that removal of outlying densities best revealed the general spatial structure of the *L. depurator* population, hence that procedure has been adopted here. The variograms were computed with the residuals from separate linear regressions of abundance with depth for each year, where densities exceeding 1.5 times the inter-quartile range were excluded.

A spherical covariance model best fitted the variograms, which were derived from the average semi-variances over superimposed 150 km lengths of coastline lagged into 13.6 to 6.5 km classes. The number of lags was varied to ensure stability of parameter estimate and avoid random fluctuations arising from fortuitous groupings of semi-variances (see Rufino *et al.*, submitted). The method of weighted least squares (WLS) was used to fit the spherical model (Cressie, 1991). WLS has been widely recommended for fitting spatial models to variograms and it is probably the most commonly used fitting method (Cressie, 1991; Webster & Oliver, 2001).

After determining the parameters of the spherical model for each year, universal ordinary kriging (kriging with depth as an external trend) was used to estimated abundance, using all the raw sample densities (including outliers). Depths over the sampled area were matched to the kriging density estimates by extrapolation from those measured during each trawl and those provided by the GEBCO data set. A grid, with a mesh size of 0.5 km, was drawn over the sampled area for the application of universal ordinary kriging. Estimated abundance at grid nodes is interpolated from measured densities at the sample points on the grid. Kriging uses the values of neighbouring data points to estimate densities at unsampled grid points (Cressie, 1991). The kriging estimate is the average of neighbouring densities weighted by the parameters of the spatial model (Petitgas, 1996).

Density and variability predictions were estimated using universal block kriging as recommended by Maynou (1998) for fisheries studies. Variability was expressed relatively as coefficients of variation either calculated from the sample data or from the kriging estimates. The difference in the coefficient of variation between the sample and kriging estimates was considered by Rivoirard *et al.* (2000) as a direct estimate of the difference in error variance between the two approaches.

VI-4. RESULTS

VI- 4.1. Variogram analysis: the spatial model

The distribution of the *L. depurator* densities (number.km^{-2}) was highly skewed (skewness varying from 2.35 in 1995 to 7.08 in 1999) and predictably non-gaussian (Shapiro test: 0.27<W<0.59, p<0.001). The modal value for each distribution was zero.

A linear relationship between depth and crab density was found in all years, hence the semi-variograms were computed from the residuals of density from linear regression on depth in each year.

The residual semi-variograms showed varying degrees of spatial structure in the *L. depurator* distribution in all but one year, 1998 (see Figure VI-1), where no spatial structure was evident (a flat variogram), the spherical model was fitted to the variogram. A 'linear' spatial covariance model was fitted to the 1998 semi-variogram. The addition of the linear trend with depth (covariate), improved the estimations and decreased the total variance of the variogram models, indicating that a large part of the spatial distribution was explained by the relationship with depth, as expected (section V).

Table VI-1 lists the parameters of the spherical models fitted for each year and Figure VI-1 shows the variogram plots. 1998 is omitted since there is no discernible spatial structure to be found. The percentage of variability explained by the fit of the model (often considered a measure of spatial dependency in the distribution) varied from 35 to a notional 100%. 1996, 2001 and 2002 showed the highest unexplained relative variability.

Figure VI-1: Semi-variograms for *L. depurator* residual (from a regression with depth) density along the Spanish coast from 1994-2003. Where appropriate, spherical models are fitted by WLS. See Table VI-1 for details on the fitted models. The diameter of the symbol is porportional to the number of pairs, although the scaling varies with the year.
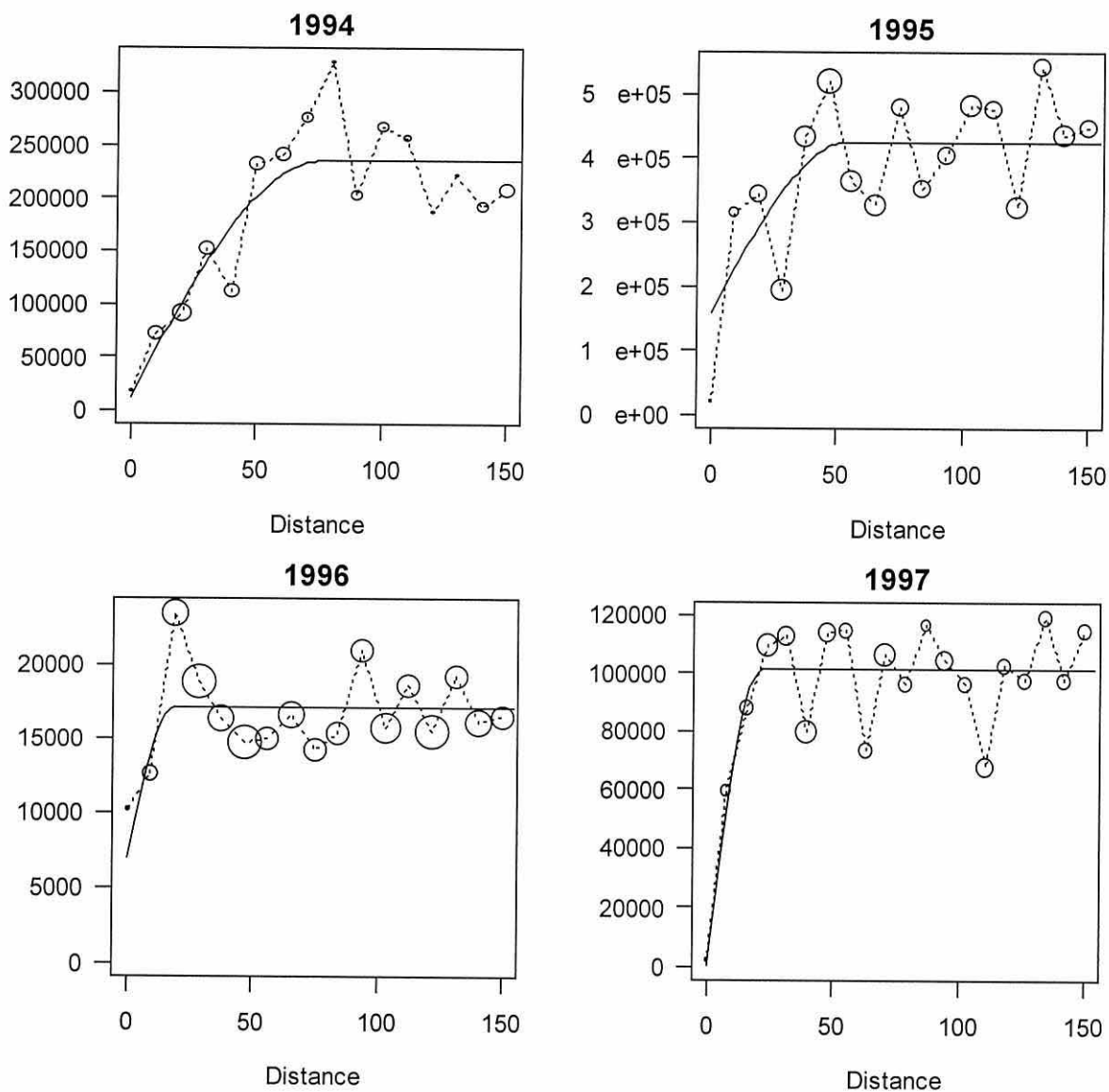
(Figure VI-1 cont.)
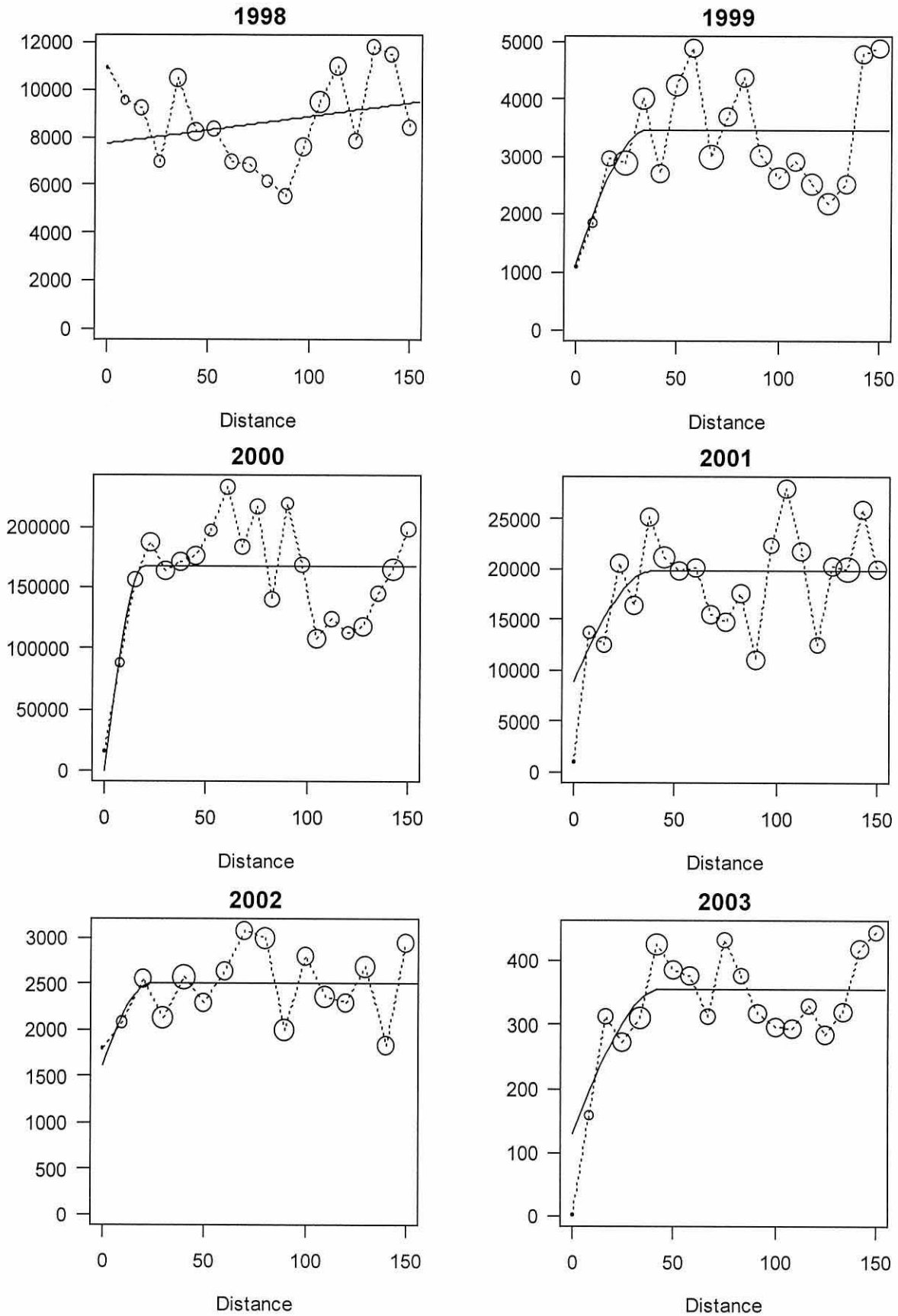
Table VI-1: Estimated parameters from the spherical covariance models fitted to the semi-variograms of Figure VI-1. SpD is the percentage of explained variability and indicates the degree of spatial dependency.

Year	Lags	Nugget	Partial sill	range	SpD
1994	16	12987	222048	75	95
1995	17	159235	266116	55	63
1996	17	6995	10121	19	59
1997	20	343	100874	22	100
1999	19	1147	2307	35	67
2000	21	0	167070	19.7	100
2001	21	8976	10781	38.0	55
2002	16	1627	879	23.6	35
2003	19	130	225	43.8	63

Figure VI-2: Variation of the estimated parameters of the spatial model fitted to variograms produced with different number of lags. The line indicates the value of the selected variogram (used in kriging).

a)

b)
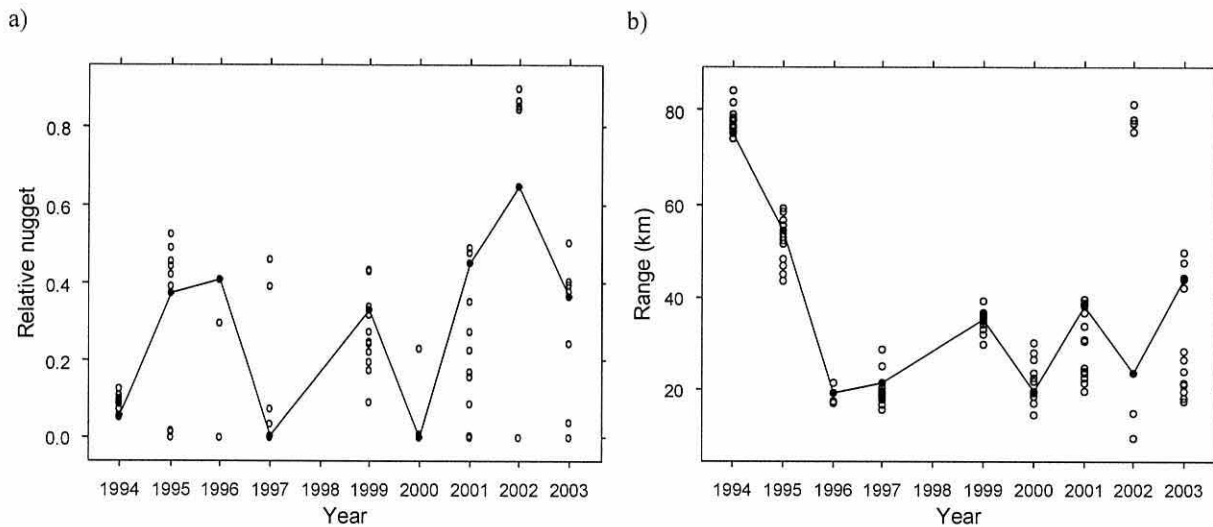
Figure VI-2 shows the outcome of the spatial model parameters when different numbers of lags were used to construct the variogram. The percentage of variability left unexplained (Figure VI-2 a) variedly from zero to around 55% in most years with no particular relationship to number of classes. In 1994 the choice of the number of lags made virtually no difference to the relative nugget whereas in 2002 unexplained variability was either excessive (~80%) or negligible depending on numbers of lags. In view of these results, no further comparison of the nugget/sill of the variogram model was done, because of its erratic nature throughout the sampled years. Figure VI-2 b shows that estimates of Range ('patch diameter') were generally more consistent with lag number (showing smaller changes with lag number) except yet again in 2002 and to some extent 2003. The lag number chosen for construction of each variogram was selected for each year on the basis of a visual criterion.

Table VI-1 indicates that the range decreased steadily from a high of 75 km in 1994 to 19 km by 1996. After this initial period, 1996 (19 km) and 1997 (22 km) showed similar ranges (Table VI-1). The range estimates then fluctuated from around 20 km to a high of 44 km with an average of 28 km. Largest estimated ranges were found during 1994 and 1995, while the smallest were observed during 1996, 1997, 2000 and 2002.

VI- 4.2. Geostatistical estimation of *L. depurator* density

Liocarcinus depurator population density changed widely throughout the sampled years (Table VI-2). Densities in excess of 600 crabs.km^{-2} were observed in 1995, 1994, 1997 and 2000. In all other years densities never exceeded 280 crabs.km^{-2} with a low of 38 crabs.km^{-2} in 2003. The mean densities estimated by kriging were between 14 and 34% lower than the sample estimates resulting from the smoothing effect of the interpolation. The coefficients of variation from geostatistics (cv$_{geo}$) were always smaller than those of the sample data (cv$_{cla}$), showing considerable decrease in the error of the estimates by geostatistical methodology (Table VI-2). The sample coefficients of variation (cv), were all in excess of 200% with the largest approaching 400% during 1997 (Table VI-2). Such is not surprising given the expo-nentially skewed nature of the abundance distributions with a modal value of zero in every year. Table VI-2 also shows that the relative variability from the Kriging density estimates were universally lower and very similar ranging from 44 to 59% (except in 2002, 13%). Once again the smoothing effect of the interpolation consistently reduces the apparent variability and to virtually the same percentage of the mean irrespective of the average value.

Table VI-2: Mean *Liocarcinus depurator* density (number.km^2) estimated for the sample data and for the univer-sal block kriging estimate, respective coefficient of variation (cv) in the Spanish Mediterranean coast. Note that 1998 was excluded. Mean density indicates the sample data and the universal block kriging estimate.

Year	cv$_{sample}$	cv$_{kriging}$	Mean density		Dif sample & kri-ging
			Sample	Kriging	
1994	2.460	0.547	690	590	15%
1995	1.955	0.506	985	744	25%
1996	2.664	0.594	161	139	14%
1997	3.885	0.463	631	534	15%
1999	3.458	0.463	107	80	25%
2000	2.018	0.543	696	580	17%
2001	2.468	0.471	205	176	14%
2002	3.841	0.128	276	199	28%
2003	2.908	0.441	38	24	34%

There was no significant correlation between patch size (variogram range) and the aver-age density (r= 0.332, N=9, p=0.383). Ranges between 20 and 75 km were estimated for

1994, 1995 and 2000, corresponding to the highest *L. depurator* densities. However, 1997 and 2000 had equally high densities of crabs but patch size was estimated as 20 km. 2003, spoting the lowest average crab density which had a range of 45 km.

VI- 4.3. Geostatistical mapping

Kriging, using the spatial models, provided interpolated densities for a smoothed and detailed visualisation of the *L. depurator* distribution along the coast throughout the 10 years (see Figure VI-3). Patchiness was an almost constant feature but varied in expression from year to year and was much less evident when annual densities were low. Figure VI-3 shows that the vicinity of the Ebro Delta and western Alborán Sea invariably show the highest *L. depurator* abundances, although the extent of these high-density patches is highly variable annually. Less predictable areas of high density are found off the northern part of the Catalonia coast (close to the Gulf of Lions), around the Cape Nao, on the coast of Valencia, Alicante and in the eastern Alborán Sea. These, more transient, patches only occur when average densities in general were high.

Figure VI-3: Kriging prediction of *Liocarcinus depurator* abundances (ind.km⁻²) in the western Mediterranea coast. See Table VI-1 for details on the models. All models were fitteed with a spherical covariance model with a linear trend with depth, except 1998 where a liner model was fitted. See Figure II-5 for locations of the sampling stations for each year. Longitude scale refers to the first left bottom graph, the remaining graphs are repetitions with the same scale. Color bar shows crab abundance levels.
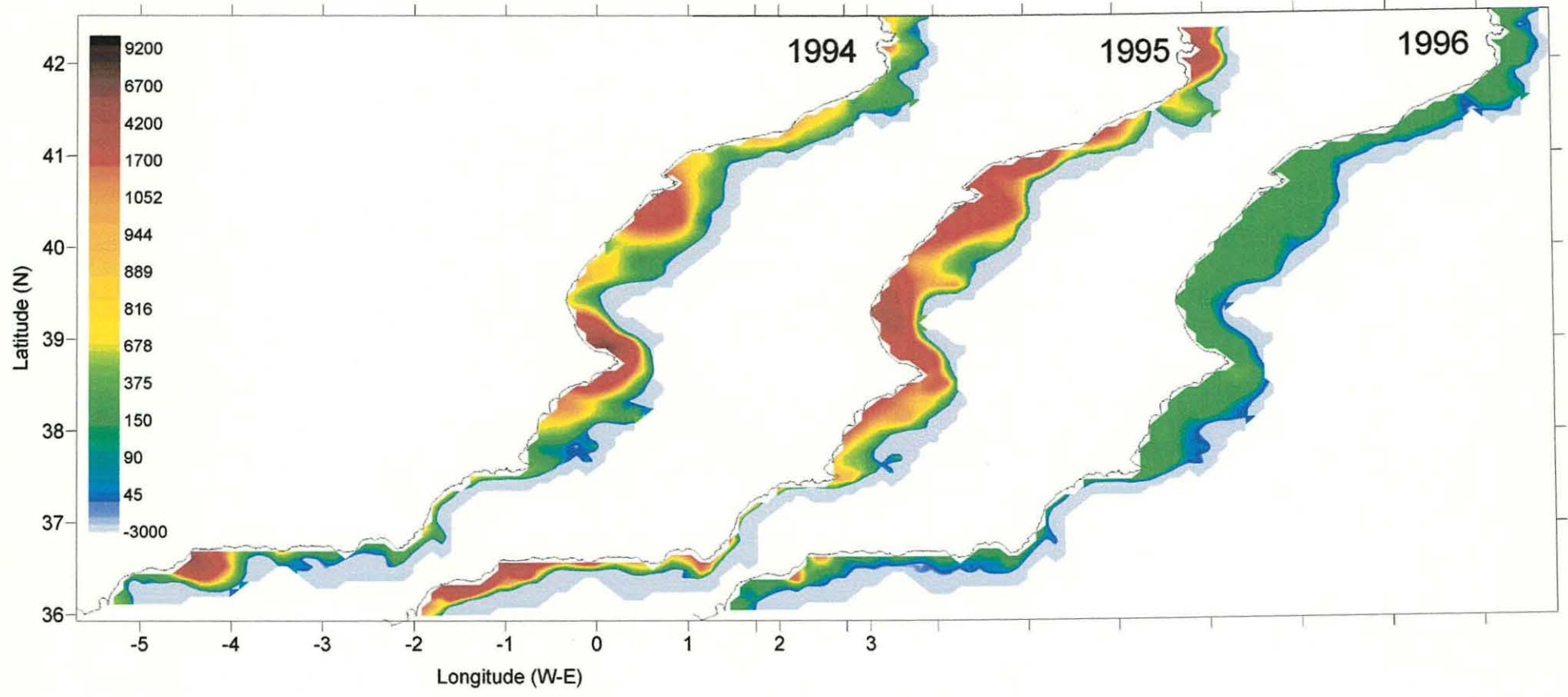
(Figure VI-3 cont.)
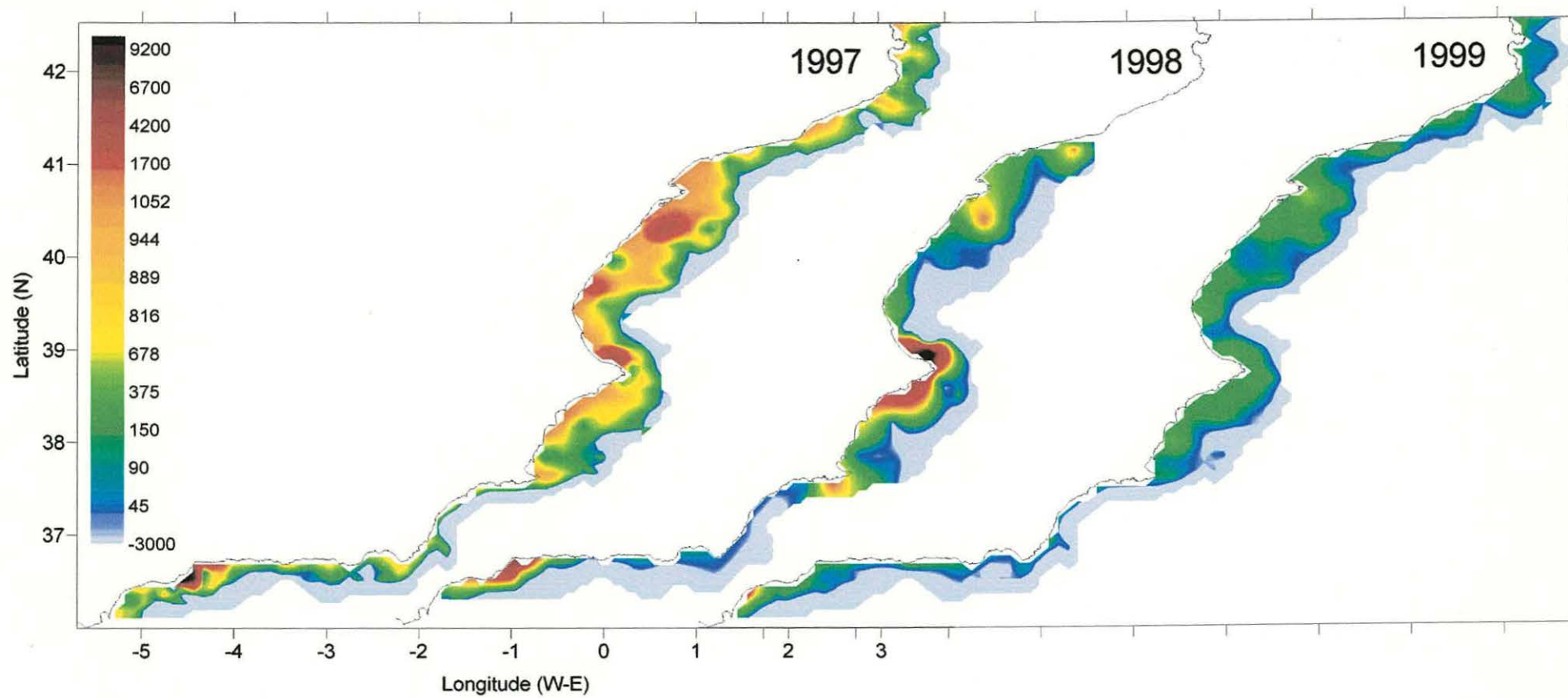
(Figure VI-3 cont.)
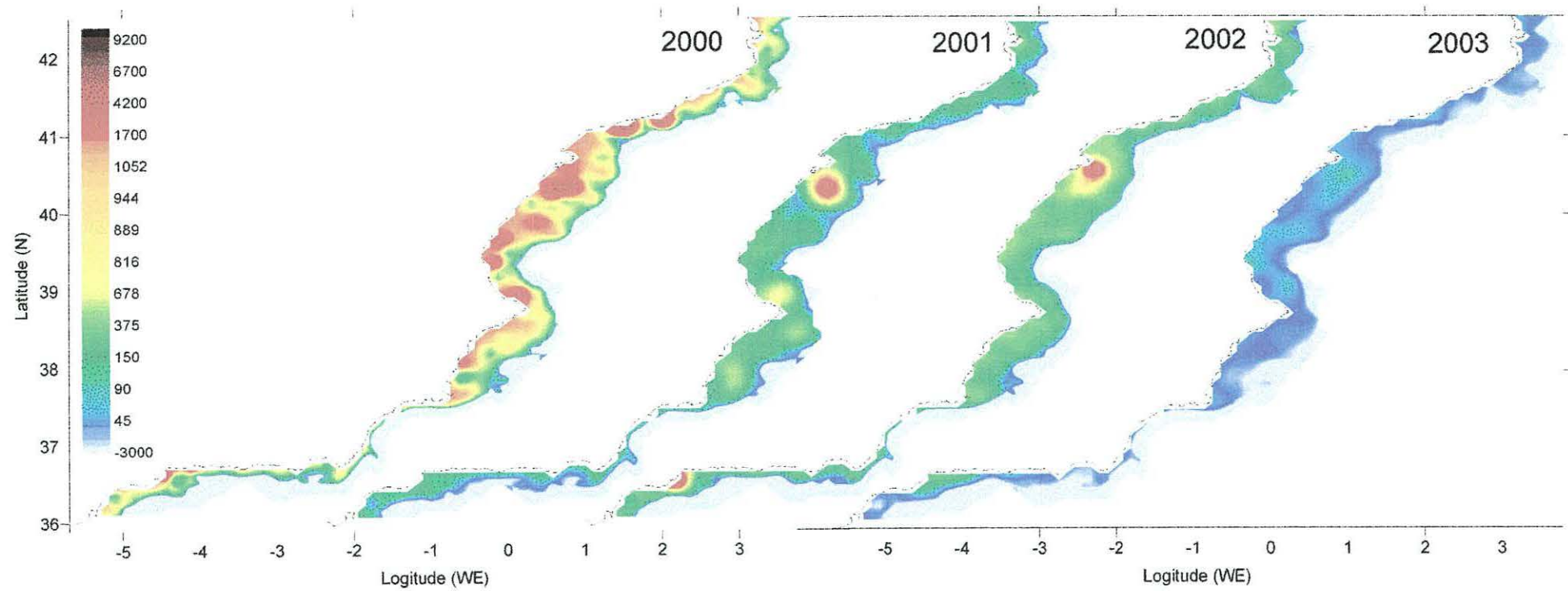
Both high-density areas in the Alborán sea (west and east) may well be related to the eddies formed by the inflow of Atlantic waters through the Strait of Gibraltar (see Figure II-11 and Figure II-12 for the location). The location of the Western Alborán *L. depurator* 'patch' corresponds to the position of an annual, upwelling-driven, high productivity region (Figure VI-3). The predictable crab patch Southeast of the Ebro Delta also corresponds to a region of high primary production. However, it is likely to be fuelled from the ouflow of the River Ebro Delta rather than eddy-driven upwelling (see section II).

The smaller Eastern Alborán crab patch is located in a region of occasional eddy formation and associated high productivity occurred. Other occasional 'patches', Cape Nao and Gulf of Lions are also influenced by unpredictable, eddy-driven upwelling and hence occasional high productivity. When annual densities reached their lowest (during 1996, 1999 and 2003), the crabs seem restricted to the Ebro River Delta and Western Alborán Sea, which may well be the most favourable. Those areas should be considered as priorities for management and conservation of the species.

VI-5. DISCUSSION

Liocarcinus depurator was found throughout the study area, from Gibraltar to Cape Creus. The areas where *L. depurator* was most often present, the Ebro Delta, Alicante and Valencia all have the largest expanse of continental shelf along the Mediterranean coast Spain. Moderate populations were observed in the West Alborán Sea and North Catalonia. The former area has a strong, nutrient rich Atlantic influence and the latter is influenced by the interaction between the Liguro-Provencal current and the numerous submarine canyons cutting the continental shelf slope. In every year, the areas with the lowest *L. depurator* densities equated to those with the narrowest continental shelves and steepest slopes.

Geostatistical analysis has been successfully applied to the distribution of *L. depurator*, although it might be considered to stretch the limits of the technique given the low sampling density relative to the sampled area, the high sample variances and exponential skewness of the density distributions. Apart from 1998, distributions from all years exhibited spatial structure once 'outlying' samples were removed. The degree of spatial dependence (i.e variance explained) ranged from 61% to 100%. The inclusion of a trend, of decreasing density with depth and the incorporation of the spatial models in the contouring process undoubtedly led to smoother and more easily interpretable contour maps of density distribution than would have been possible with the sample data alone.

The density and size structure of *L. depurator* populations is known to be related to depth (Abelló, 1993; Abelló *et al.*, 1988; Mori & Zunino, 1987). However, González-Gurriarán *et al.* (1993), admitting the influence of depth at larger scales, considered that it had little influence on *L. depurator* densities within their study area along the Galician coast. A similar small scale study within the Mediterranean has shown that *L. depurator* densities vary considerably with depth, peaking around 100 m and declining quadratically to greater depths. Sulivan (1991) demonstrated the effectiveness of incorporating a population delimiter, such as depth, in geostatistical analysis of fisheries data. The current study also highlights the efficacy of including such a delimiter (depth in this instance) and recommends the incorporation of such in any spatial analysis of marine populations, wherever depth is relevant to the species distribution. The shape of the current study area was neither linear nor a regular grid and the realistic appearance of geographic trends in population were better represented when density relationships with depth were included.

The number of lags used to create the semi-variograms had a considerable influence on the shape of the spatial model fitted. Such, presumably, resulted from the small number of data points in relation to the area sampled and the distribution of the data, i.e. highly skewed and non normal. In particular, the proportion of explained variance was extremely sensitive to lag number and nothing could be gained from annual comparisons. On the other hand, the range was much less sensitive and sensible inter-annual comparisons were possible. Estimated ranges varied between 19 and 75 km over the ten years but with no consistent pattern and only a superficial relationship to crab density.

Previous studies of *L. depurator* populations on the Atlantic continental shelf (Galicia) found patch sizes between 14 and 22 km (González-Gurriarán *et al.*, 1993) with a much smaller range of 3 km for crabs living in the Ria de Ferrol (Freire *et al.*, 1993). In the Ebro Delta (Mediterranean) a small-scale study found the *L. depurator* patch size to be 11 km (section V). It would appear that patch size estimation is sensibly related to study area size. In the Ria de Ferrol study maximum variogram distance was 8 km and that for the Ebro Delta river was 25 km in comparison to the 150 km of the present study and 60-120 km on the Atlantic shelf. In the southwestern Adriatic Sea, Ungaro *et al.* (1999b) estimate *L. depurator* patch ranges of 70 km in the spring and 160 km in the autumn (0.48° * 60 min * 1.852 km = 53.34 km, which for the exponential model used in that study, the effective range = 3 * range (Cressie, 1991): 53.34 km * 3 = 160 km) in autumn and 69.67 km (as before: 0.209° * 60 min * 1.852 km * 3 = 69.67 km). Their spring range values are equivalent to those of the current study in 1994/5 even though their sample area is much smaller. Clearly the size of the sampled area and sampling unit (i.e. area covered during the trawl) can determine the detail of the

spatial structure observed. Large areas, such as in the current study, may cover many patches but with poor resolution in each patch. A smaller scale study of a patch will give much more detail on the spatial structure of each patch. A combination of both patch structure and patch distribution is thus necessary for improved interpolation of population densities over large areas.

In the present study considerable variation in the patch size was found throughout the study. Large patch size estimates were obtained at the start of the project (1994/5) when sampling protocols were being established and sampling density (number of samples per unit area covered) was relatively low. Large range estimates were also obtained in 2002/3 when the project protocols were well established. The large range estimates were thus not artefacts of establishing the project. The lack of trend in range either with crab density or year possibly reflects the sampling strategy in relation to the methods used. 2003, the lowest density year, shows a relatively high range but the densities throughout the area are so low that the concept of a 'patch' is hardly tenable. 1996, 1999 and 2003 are similarly low density years but only 1999 and 2003 have moderate ranges. Any interpretation of inter-annual variation in range would require a much more detailed examination of individual patches than was possible from the current survey.

When annual *L. depurator* densities were low (during 1996, 1999 and 2003), the crabs were most abundant in Ebro River Delta area and the Western Alborán Sea. These areas are presumably more favourable areas combining high productivity with extensive shelf mudflats. As such they must represent key areas for continuation of the species during years with worst environmental conditions for the species. Conservation or management policies must be directed towards those areas if they are to be successful.

Annual variations in meteorological conditions (e.g. temperature) and oceanographic features can influence the survival of crabs, both adults and larvae, hence, their densities. Such influence may not be directly exerted in the same year, but may affect egg or larval development hence alter recruitment in later years. For example, a constant north-eastern winds influenced recruitment of the *Chionoecetes bairdi* (tanner crab), 6 and 7 years later (Rosenkranz et al. 1998 in Rosenkranz *et al.*, 2001)).

VII. Small-scale non-linear geostatistical analysis of *Liocarcinus depurator* (Crustacea: Brachyura) abundance and size structure in a western Mediterranean population.

VII-1. ABSTRACT

The small-scale spatial distribution of density and biomass of the crab *Liocarcinus depurator* off the Ebro Delta was analysed using universal kriging (non-linear geostatistics), considering depth as an external trend. In order to understand the spatial distribution of crab size, a third variable was created from the residual weights of the non-linear regression between biomass and density. Variogram analysis of crab density and residual weights of the biomass/density relationship presented a quadratic relationship with depth, while biomass showed a linear relationship with depth. All experimental variograms were fitted to spherical models. The patch size (range) found was 11 km for density, 15 km for biomass and 21 km for the residual weights variable. The spatial distribution of eight sediment variables (temperature, redox potential at 1 cm and 6 cm depth, carbonate contents, median grain size, sediment sorting and organic matter contents) was studied. The maps obtained were compared with the distribution of *L. depurator* using Mantel and partial Mantel's tests. Distributions were positively associated with sediment variables, particularly with temperature, organic matter content and redox potential. Density and biomass, were negatively correlated with sediment sorting and with concentration of carbonates, although showing low correlations. Additionally, the size structure of the population was significantly correlated with grain size (φ), hence larger individuals occurring in finer sediments, while juveniles were preferably found in areas with very fine sand sediments. The correlation of density and biomass were significantly correlated with temperature, redox potential and organic matter.

VII-2. INTRODUCTION

Patchy distributions of individuals in marine benthic systems can be related to local environmental conditions as well as to biotic factors such as competition and predation (Palmer, 1988; Whittaker & Levin, 1977). For example, predators may more readily locate prey items in some habitats than others, hence reduce prey abundance differentially between habitats (Southern & Lowe, 1968). Additionally, the physical environment, for example temperature, salinity and sediment characteristics, has been shown to determine small-scale distribution in

benthic crabs (e.g. Vernberg & Vernberg, 1983). Sediment grain size, which is determined by hydrodynamic sorting mechanisms, and organic content are considered the two most influential characteristics for determining occupancy by marine benthos (Gray, 1981).

Surveys designed to assess the density of benthic organisms often do not take into account the spatial heterogeneity of the habitats or try to account for it by implementing differential habitat sampling, often referred to as stratified random sampling (Petitgas, 1996). However, empirical evidence suggests that the existence of environmental heterogeneity at different spatial scales must induce autocorrelation between pairs of samples, producing biases in density estimates (Petitgas, 1996). Further, there is interest quantifying the interrelationships between samples since it can provide clues to the spatial structure of benthic populations and the potential factors determining such. In this context, the use of geostatistics has been advocated by several authors as a useful tool to describe and model spatial distribution in benthic organisms (e.g. Fernandes & Rivoirard, 1999; Maynou, 1998; Maynou *et al.*, 1996; Petitgas, 1993; Petitgas, 1994; Petitgas, 1996; Rivoirard *et al.*, 2000; Sullivan, 1991). Conan (1985) first introduced geostatistical techniques in marine biology, using kriging to produce biomass estimates and isodensity contour maps of *Placopecten magellanicus* (scallop) distribution.

Most applications of geostatistics to marine organisms are on fish species and were recently reviewed by Petitgas (1993; 2001). However, the application of geostatistics to crustacean populations is still limited (Freire *et al.*, 1992; Freire *et al.*, 1991c; González-Gurriarán *et al.*, 1993; Maynou, 1998; Maynou *et al.*, 1996; Maynou *et al.*, 1998; Simard *et al.*, 1992). Additionally, most of those applications were linear geostatistics and ordinary kriging, no data transformation or correlation with ancillary variables which might improve parameter estimates. Furthermore, when the response variable is not stationary, non-linear geostatistics is more appropriate (Cressie, 1991).

Differences in spatial distribution of juveniles, females, males, berried females (for example) of the same species, have often been reported in the literature (e.g. Abelló *et al.*, 1997; Abelló *et al.*, 1990b; Ardizzone *et al.*, 1990; Rossi & Costantini, 2000) but seldom analysed through geostatistics (Comeau *et al.*, 1998; Lembo *et al.*, 2000a; Maynou *et al.*, 1998). Furthermore, different scales of spatial structure may separate different classes within a given species, as shown for example in *Chionoecetes opilio* (snow crab), where an important spatial segregation was detected by sex and size in the Gulf of Saint Lawrence (Canada) using geostatistics (Comeau *et al.*, 1998). The spatial distribution of the shrimp *Parapenaeus longirostris* and *Aristeus antennatus* was studied by Lembo *et al.* (1999; 2000a; 2000b) in the Thyrrhenian Sea (Italy). They applied cross-variograms, co-kriging and considered depth as a

covariate to obtain density estimates. Three higher densities locations persisted from 1995 to 1997 (Lembo *et al.*, 1999).

Liocarcinus depurator is the most common and abundant brachyuran crab on trawled muddy bottoms of the continental shelf in the western Mediterranean (Abelló, 1993; Abelló *et al.*, 2002; Abelló *et al.*, 1988; González-Gurriarán *et al.*, 1993; Mori & Zunino, 1987). Given its abundance and the fact that it is a predator of mobile benthic and epibenthic organisms, it may prove to be a "keystone" species in the community (Abelló & Cartes, 1987; Mori & Manconi, 1989). *L. depurator* is distributed along the eastern Atlantic coasts from Mauritania to Norway, and throughout the Mediterranean (d'Udekem d'Acoz, 1999; Zariquiey-Álvarez, 1968), showing a wide bathymetric range (continental shelf and upper slope). It occurs on several types of substrata, especially on muddy and muddy-sandy bottoms (Minervini *et al.*, 1982). Abelló (1993) showed a trend for bigger crabs, both males and females, to be found at greater depth in a population off the Catalan coast. Recruitment took place mainly on the shallow continental shelf (25-50 m), but generally over a wider range. In *L. depurator*, geo-statistical analyses have been applied by Freire *et al.* (1991b) and González-Gurriarán *et al.* (1993) off the Atlantic Iberian coasts and by Ungaro *et al.* (1999b) in the southwestern Adriatic Sea. Both studies report that *L. depurator* are aggregated spatially in patches, both on the Galician continental shelf and in the Adriatic. Depth, bottom steepness and sediment characteristics have been shown in these studies as factors affecting the spatial structure of *L. depurator*.

The objectives of the present work were to analyse the distribution of *L. depurator* in a population located off the Ebro delta in the western Mediterranean and to relate the distribution patterns to observed environmental parameters. It was expected that the sediment characteristics would significantly affect *L. depurator* distribution. Furthermore, this study aims to illustrate the use of non-linear geostatistics and to indicate how this technique could be more widely applied to the study of the spatial patterns of benthic species.

VII-3. MATERIAL AND METHODS

VII- 3.1. Survey

A trawl survey (GEODELTA) was conducted over muddy bottoms off the Ebro delta continental shelf and slope (40°20'N to 41°00'N, NE Spain, Figure II-1) using R/V "García del Cid". A regular grid 1 by 2 nautical miles was set parallel to the coast and a start location for each tow was randomly selected within each cell. An area of oil production platforms in the

south was not sampled. 72 stations were sampled between 7 and 15 April 1994. The water depth varied from 83 to 713 m across the sampled sites. The northern part of the study area was characterised by a narrow shelf (8-10 km wide) having a gentle slope seaward which is cut by deep submarine canyons. South of ~ 40°50' N the shelf becomes progressively wider (38-40 km) and the slope becomes steeper with fewer canyons.

The sampling gear was a modified otter trawl drawn by a single warp ('Maireta System Trawl': Sardà *et al.*, 1994). The codend stretched mesh width was 12 mm in order to retain small individuals not normally caught by commercial fishing gear. The working dimensions of the trawl mouth were measured acoustically (SCANMAR) and averaged 13.4 m across by 2.0 m high. The effective trawling time was 15 minutes and trawls were always made parallel to the depth contours. Towing speed varied between 2.3 and 2.7 knots (mean 2.5 knots). Start and end locations for each tow were taken by calibrated GPS. The actual surface covered by each tow was computed from the GPS and the SCANMAR readings. Further details of the survey can be found in section II.

Figure VII-1: The relationship regression between density (crabs.ha^{-1}) and biomass (kg.ha^{-1}) with fitted line. biomass = 5.69 × abundance$^{1.31}$, r^2 = 0.9074).
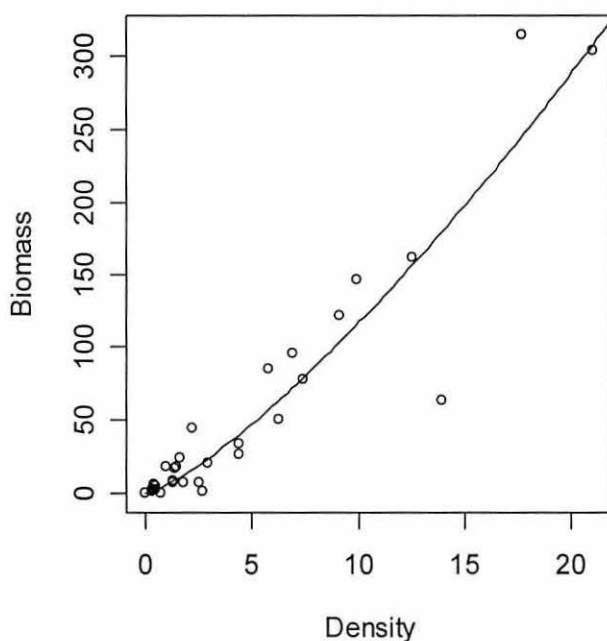
The total catch of *L. depurator* was counted, weighed and the carapace length of each crab was measured. Density was computed from the total surface covered by each tow as number of individuals.ha^{-1} and biomass as kg.ha^{-1}. Three biological variables were considered: density, biomass, and the residual weights of the non-linear relationship between biomass and density, as an indicator of the relative size of the individuals (Figure VII-1). The re-

sidual weights from the weight/length relationship give a rough indication of the size structure of the population. Positive residuals indicate higher than average weights/unit crab (i.e. mainly large individuals) whilst negative residuals indicate the opposite.

Sediment samples were collected using a van Veen grab (Gray, 1981) on every second trawl, except on the continental shelf, at depths shallower than 200 m, where sediment hetero-geneity was presumed higher and the collection of one sediment sample per tow was at-tempted. Sediment samples were analysed following the methodology presented by Maynou & Sardà (1997) and Alonso *et al.* (1999). The surface sediment temperature (T, °C) and the redox potential at 1 and 6 cm from the sediment surface (R1 and R6, mV) were measured on-board using a double-joint, multimeter electrode (Orion Research model 250A) immediately after the sample collection. Furthermore, the differences between R1 and R6 were analysed, which represents the vertical difference in the redox potential between 1 cm and 6 cm. Sedi-ment samples were stored at −20 °C for later laboratory analyses. The redox potential is a measure of the lack of oxygen in the sediment and, for marine sediments, is usually negative with higher negative values indicating more reduced sediments. Highly negative redox poten-tial also generally indicate sediments with higher organic content. Normally, marine sedi-ments are structured in layers when undisturbed, and the deeper redox potential measurements show higher negative values than those near the surface. Grain-size analysis was carried out using a SEDIGRAPH 5000D for the fine-grained fraction (< 50 μm) and sedimentation tube analysis for the coarse-grained fraction. For each sample, the proportions of sand (62.5-1000 μm), silt (2-62.5 μm) and clay (0.06-2 μm) were determined. The grain-size distribution of each sample was summarised also by its median, $\varphi = -\log_2$ (median grain size in mm) (Gray, 1981), and its sorting coefficient Inclusive Standard Deviation (IGSD; Gray, 1981). Small values of IGSD indicate a well-sorted sediment and large values of IGSD indicate poorly sorted sediments (Maynou & Sardà, 1997). The carbonate content (% of CO_3 by volume) for each sediment sample was determined using a Bernard calcimeter, following the methodology presented by Vatan (1967).

VII-4. RESULTS

Density and biomass of *L. depurator* were significantly correlated (biomass = 5.69 × abun-dance$^{1.31}$, r^2 = 0.9074, DF = 69, p < 0.0001) by non-linear regression (Figure VII-1). The re-sidual weights from the relationship, however, were not normal. No empirical transformation improved normality.

The results of the Mantel and partial (extracting the effect of depth) Mantel tests (Table VII-1) indicated that density, biomass, residual weights, carbonate and sorting index (IGSD) were spatially aggregated. By removing the effect of depth (partial Mantel test), aggregation was still evident, although the spatial correlation (r) decreased. Thus depth was not the sole structuring variable.

Table VII-1: Results of the Mantel test and the partial Mantel (extracting the effect of depth) using Kendall's correlation index. Significant spatial correlation (0.95<p<0.05) is highlighted in bold.

	simple		Partial	
	r	p	r	p
Abun-dance	**0.166**	**<0.001**	**0.139**	**0.007**
Biomass	**0.137**	**0.015**	**0.117**	**0.022**
Residuals	**0.142**	**0.007**	**0.121**	**0.019**
Temp	0.0670	0.0509	0.0306	0.1859
R1	0.0260	0.2421	0.0304	0.2161
R6	0.0596	0.0779	0.0632	0.0751
R1R6	-0.0333	0.7680	-0.0303	0.7423
CO$_3$	**0.1441**	**0.0021**	**0.1275**	**0.0036**
φ	0.0522	0.1348	0.0229	0.2914
IGSD	**0.2154**	**0.0001**	**0.2006**	**<0.0001**
OM	-0.0519	0.9109	-0.0679	0.9697

The minimising function for the variogram models fitted (spherical, Gaussian, and exponential) (Table VII-2) indicated that the spherical model was the most appropriate, since it gave the lowest minimising function. Density and residual weights showed a quadratic relationship with depth, while the relationship of biomass with depth was found to be linear. The patch diameter (range) found was 15 km for density, 11 km for biomass and 21 km for the residual weights.

The degree of spatial dependence (Robertson & Freckmann, 1995) was high and varied between 82 and 100 %, indicating that most of the total variance could be explained by the variogram models. Figure VII-2 presents the experimental variograms with their selected model fits.

Contour maps from kriging with a depth trend and estimated variances are presented in Figure VII-3. Variance estimates from the kriging interpolations are roughly equivalent over the whole area. In the north of the study area, two main patches of high density and biomass were found around the 100 and 200 m depth contours (patches labelled 'a' and 'b' in Figure VII-3). A central area (around 200 m depth) of relatively high density and biomass was also observed 15 km north of the main submarine canyon. *L. depurator* showed greater density and biomass in shallow than in deeper waters within the sampling area.

Table VII-2: Models fitted with weighted least squares to the experimental variograms, produced for each biological variable. Saptial dependency (SpD) indicates the % of the variance explained by the model: (1- nugget/sill)×100; 1st depth indicates a linear trend with depth, 2nd depth a quadratic trend. Lin: linear model, Gau: Gaussian model and Sph: Spherical model. Selected model for kriging is in bold.

		Nugget	Sill	SpD	Range	Min. funct.
Abundance						
No trend	Sph	2.13	16.69	87	21.88	1.3×10^4
	Gau	4.64	14.16	67	10.66	1.3×10^4
	Exp	0.00	21.20	100	10.25	1.4×10^4
1st depth	Sph	2.39	10.28	77	14.80	0.7×10^4
	Gau	4.20	8.51	51	7.50	0.7×10^4
2nd depth	Sph	1.88	10.52	82	14.53	0.6×10^4
	Gau	3.80	8.66	56	7.43	0.6×10^4
Biomass						
No trend	Sph	73.66	3282.38	98	14.49	3.8×10^8
	Exp	0.00	3531.88	100	6.16	4.2×10^8
1st depth	Sph	0.00	2661.70	100	10.64	3.0×10^8
2nd depth	Sph	0.00	2626.25	100	10.78	3.2×10^8
Residuals						
No trend	Sph	39.92	296.21	87	20.18	1.6×10^7
	Exp	0.00	359.57	100	8.25	1.7×10^7
1st depth	Sph	39.84	296.14	87	20.16	1.7×10^7
2nd depth	Sph	43.18	291.86	85	20.49	1.6×10^7

Figure VII-2: Experimental variogram and respective spherical model fitted with weighted least squares (the size of the markers is proportional to the number of pairs divided by the median number of pairs).

Abundance
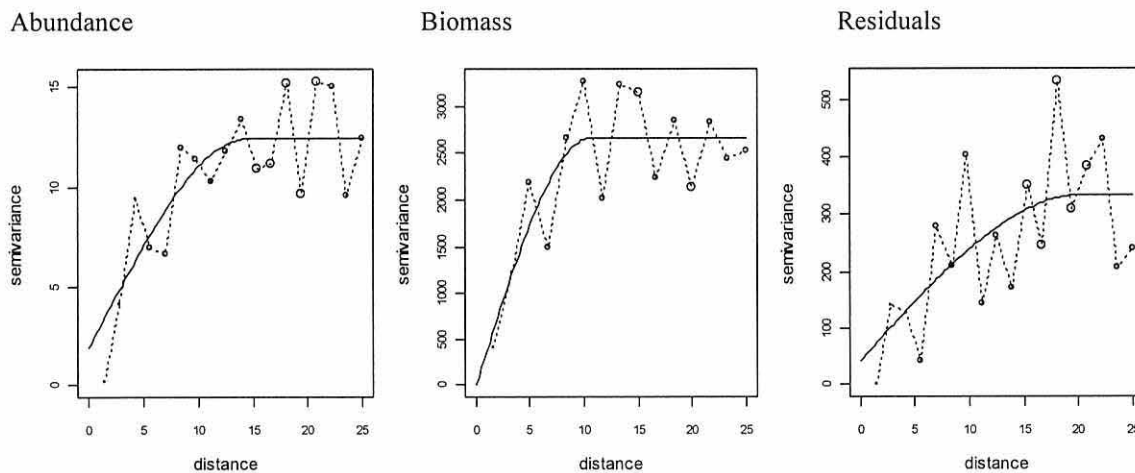
Biomass

Residuals

Figure VII-3: Maps of the biological variables: abundance (crabs.ha^{-1}), biomass (kg.ha^{-1}) and residual weights, produced with kriging with a depth trend, and estimation variances (below). Contour depth lines, from right to left 100 m, 200 m, 400 m and 600 m. Dashed area corresponds to oil production platform exclusion zone. a and b, indicate two patches with greatest densities.
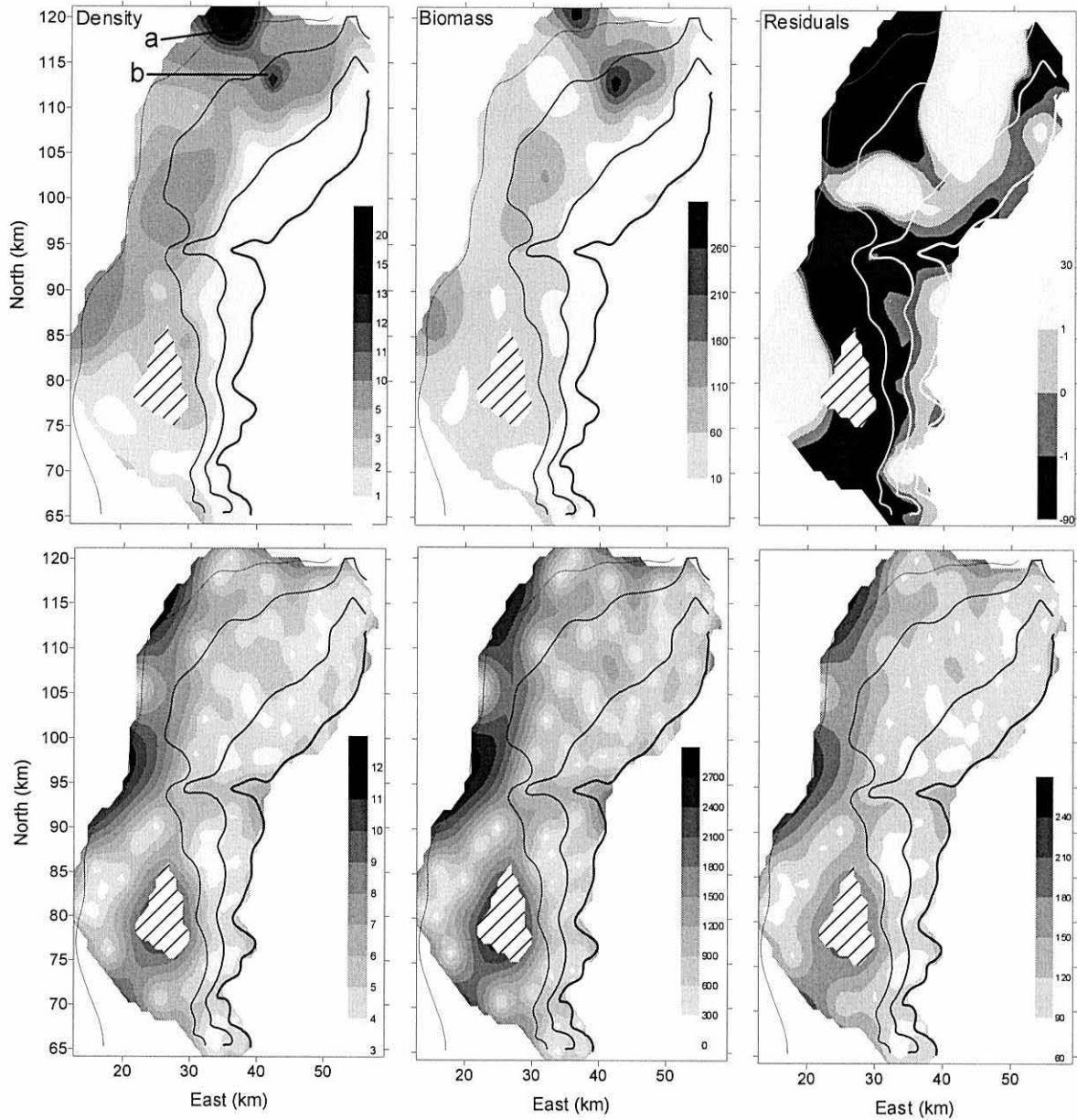
Figure VII-4: Relative frequency of *Liocarcinus depurator* carapace length (CL) in two trawls (a and b in Figure VII-3) with similar number of animals measured (respectively 30 in the black bars (a) and 32 crabs in the grey bars (b)), from two patches in distribution (see Figure VII-3).
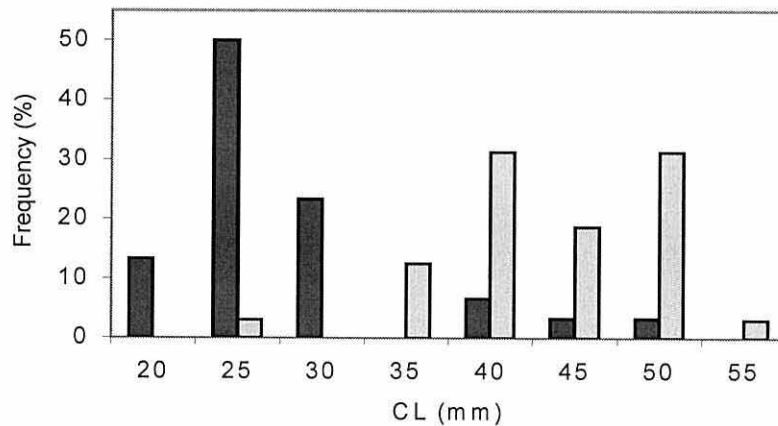
The residual weights show that, especially in the northern area with highest density and biomass, greater abundances of smaller individuals were present at shallower depths (patch 'a'), while the larger animals were found in the deeper area (patch 'b')(Figure VII-4). Deeper than 400 m, the residual weights map should be interpreted with care, since density was lower, and the residuals obtained may not be completely representative.

The estimated spatial model (i.e. selected by the lowest minimising function) for the sediment variables is presented in Table VII-3. Depth, temperature, R6, R1R6, carbonates and IGSD were fitted to a linear variogram model. Organic matter and R1 showed a spherical variogram model whereas φ presented a Gaussian model, all of them with a quadratic trend with depth. The actual range of a Gaussian model is the squared root of three times the range (Cressie, 1991). Whenever depth was used as a covariate, kriging with external drift was used, while for the remaining variables, ordinary kriging was performed (Figure VII-5). Sediment temperature showed a trend with depth, from 12.2° at the surface till 13.6° at 700 m, due to the effect of water salinity on density, since slightly warmer but more saline waters were found deeper. The redox potential at 1 cm depth (R1) showed maximum values (-8 mV to -310 mV) close to the canyon area and in the southern region, although the overall distribution was very patchy. R6 also showed a patchy distribution raging from -105 mV to -370 mV. Carbonate concentration and IGSD showed a similar pattern of distribution, with lower values in the north (carbonate content range: 23.0-41.1%; IGSD range: 1.7-3.5) and larger values in the south. Organic matter content of the sediment showed a positive trend with depth, and was particularly high around the large canyon present in the study area. Even though temperature, R1, R6 and φ did not present a significant spatial autocorrelation when using both Mantel tests (p > 0.05), the analysis of the variograms of R1 and φ clearly showed a spatial structure (Table VII-3).

Figure VII-5: Maps of the sediment variables. Temperature (°C), φ and Organic matter (%) were produced with kriging with external trend while the maps of R1 (mV), R6 (mV), Carbonates (%) and IGSD were produced with ordinary kriging. See Table VII-3 for the values of the variogram models and section II-1 for further details on the sediment variables. Contour depth lines, from right to left 100 m, 200 m, 400 m and 600 m.
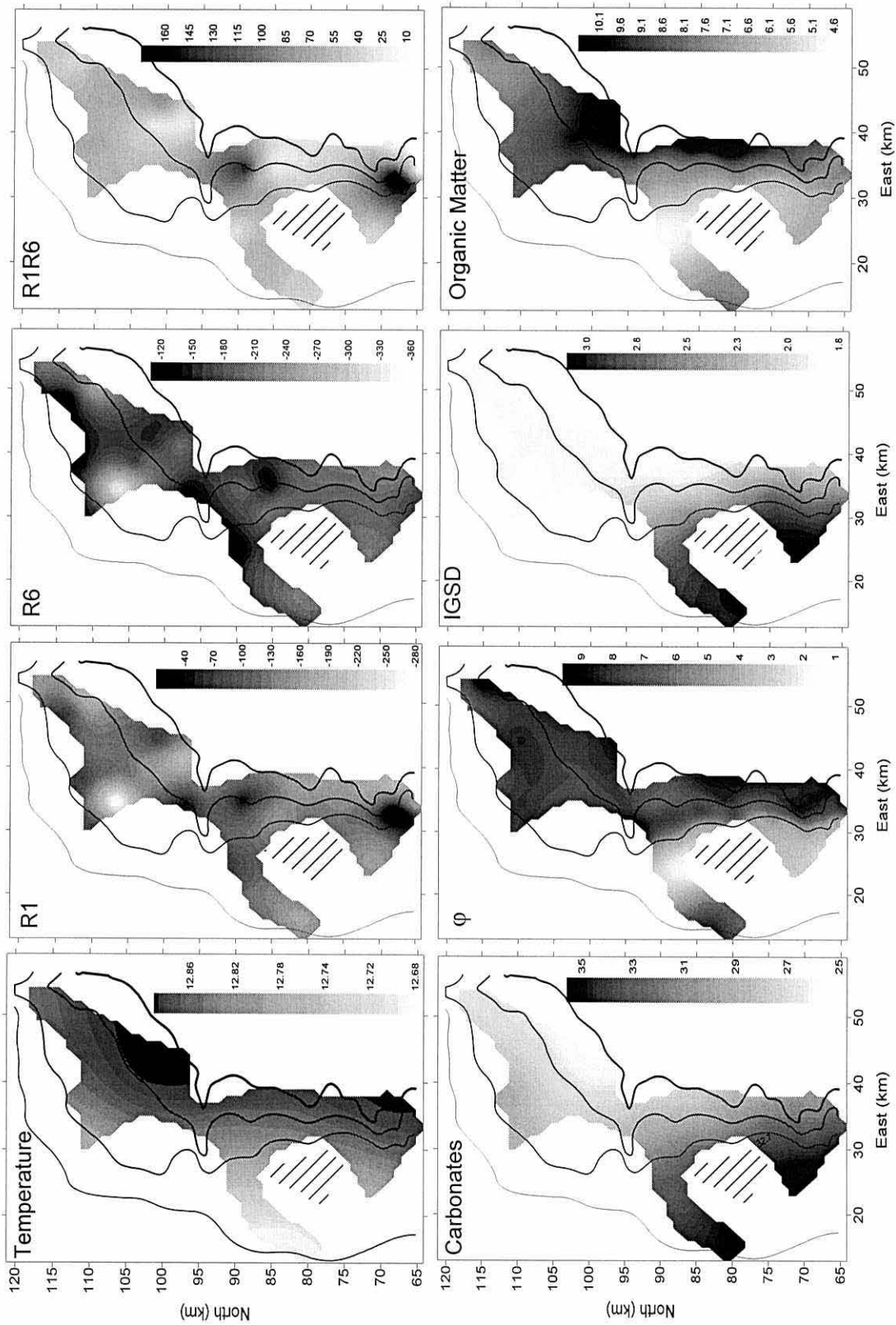
Table VII-3: Models fitted with weighted least squares to the experimental variograms, produced for each sediment variable. *Spatial dep.* indicates the % of the variance explained by the model: (1- nugget/sill)×100; 1st depth indicates a linear trend with the covariate depth, 2nd depth a quadratic trend. In the linear variogram models, the value range/slope, indicates the slope, otherwise the range. Lin: linear model, Gau: Gaussian model and Sph: Spherical model. Abreviations of the variable are explained in the Material and Methods (section II-1).

Variable	Model	Covariate	Nugget	Sill	Spatial dep.	Range or slope
Depth	Lin	No trend	372.361			1999.519
Temperature	Lin	No trend	0.041			0.005
R1	Sph	2nd depth	0.000	3253.730	100	5.950
R6	Lin	No trend	2140.783			1.000
R1R6	Lin	No trend	1555.870			1.000
CO_3	Lin	No trend	15.910			0.540
φ	Gaus	2nd depth	0.000	2.005	100	7.534
IGSD	Lin	No trend	0.124			0.012
OM	Sph	2nd depth	0.994	1.989	100	20.113

Table VII-4 shows the spatial correlation between the biological variables and sediment variables, for sampled and kriged estimates. The low number of sediment samples analysed, can be the reason for the discrepancies in the correlation results of sampled values and kriged estimates. The Mantel test using Kendall's correlation index showed that all sediment variables were significantly correlated with at least one biological variable, when the kriged estimates were used, but the degree of overlap (*r*) varied greatly (Table VII-4). The spatial overlap of R1R6 and IGSD with density, carbonates with biomass and carbonates and IGSD with residual weights were not significantly correlated (Mantel tests), but when extracting the effect of depth (partial Mantel test) the correlation became significant. The opposite occurred between carbonates and φ with density, in which the correlation was due only to the spurious effect of depth, since when depth was extracted from the relationship, the overlap became non-significant (Table VII-4). These results reinforce the importance of the incorporation of depth into the analysis, in particular when using the partial Mantel test.

The partial Mantel test, using the kriging estimates, showed that temperature, redox potential (R1 and R6) and organic matter were positively correlated with both density and biomass of *L. depurator* whereas IGSD and R1R6 were negatively correlated with them, thus indicating that these sediment variables are determinant for *L. depurator* distribution. Residual weights, were significantly correlated with all sediment variables except for R1 and R1R6; grain size φ was only significantly correlated with residual weights, thus indicating that it only affected the differential distribution of adults and juveniles, but not that of biomass or density (Table VII-4).

Table VII-4: Mantel and partial Mantel correlations of the sample data and estimated kriging values (limited to the sampled area) between abundance (N.ha^{-1}), biomass (kg.ha^{-1}) and residuals with sediment variables (temperature, R1, R6, R1R6, Carbonates, φ and IGSD) and with each other. ($p<0.05$, indicate significant overlapping). Significant spatial correlation ($0.95<p<0.05$) is highlighted in bold, if negative in italics. Abreviations of the variable are explained in the Material and Methods (section II-1).

Biological	Sediment	Kriged estimates			
		Mantel		Partial Mantel	
		r	p	r	p
Abundance	Temperature	**0.3826**	**<0.0001**	**0.1885**	**0.0011**
	R1	**0.2875**	**<0.0001**	**0.1567**	**0.0032**
	R6	**0.4105**	**<0.0001**	**0.2729**	**<0.0001**
	R1R6	-0.0700	0.9070	*-0.1047*	*0.9814*
	CO$_3$	**0.0581**	**0.0479**	-0.0474	0.9269
	φ	**0.1050**	**0.0226**	-0.0484	0.8116
	IGSD	-0.0178	0.6448	*-0.1231*	*0.9968*
	OM	**0.3673**	**<0.0001**	**0.1619**	**0.0002**
Biomass	Temperature	**0.3059**	**<0.0001**	**0.1363**	**0.0070**
	R1	**0.2392**	**0.0001**	**0.1246**	**0.0106**
	R6	**0.4017**	**<0.0001**	**0.2874**	**<0.0001**
	R1R6	*-0.1068*	*0.9824*	*-0.1344*	*0.9972*
	CO$_3$	0.0198	0.2463	*-0.0657*	*0.9794*
	φ	0.0639	0.1052	-0.0592	0.8681
	IGSD	*-0.0728*	*0.9505*	*-0.1574*	*0.9998*
	OM	**0.3067**	**<0.0001**	**0.1334**	**0.0003**
Residuals	Temperature	**0.3619**	**<0.0001**	**0.2307**	**<0.0001**
	R1	**0.1946**	**0.0009**	0.0895	0.0508
	R6	**0.2438**	**0.0001**	**0.1177**	**0.0162**
	R1R6	0.0024	0.4619	-0.0074	0.5340
	CO$_3$	0.0143	0.2998	*-0.0579*	*0.9623*
	φ	**0.2036**	**<0.0001**	**0.1188**	**0.0132**
	IGSD	-0.0333	0.7642	*-0.0982*	*0.9798*
	OM	**0.3180**	**<0.0001**	**0.1747**	**<0.0001**

Figure VII-6 shows the spatial Mantel correlogram between the environmental variables and the distance between samples. Significant correlations were observed only for shorter distances, in all cases except with the redox potential (R1, R6 and R1R6), which was correlated at larger distances, and depth, which presented significant correlation both for shorter and larger distances. Temperature, Carbonates and IGSD showed significant correlations till larger distances (15-20 km).

Figure VII-6: Mantel spatial correlogram between environmental variables and *Liocarcinus depurator* density. Significant correlations (10000 permutations; p ≤ 0.05) are indicated by closed circles and not significant by open circles. Car: carbonates; temp: temperature; F: φ; IGSD: sorting coefficient; MO: organic matter. Further details on the sediment variables are explained in the Material and Methods (section II-1).
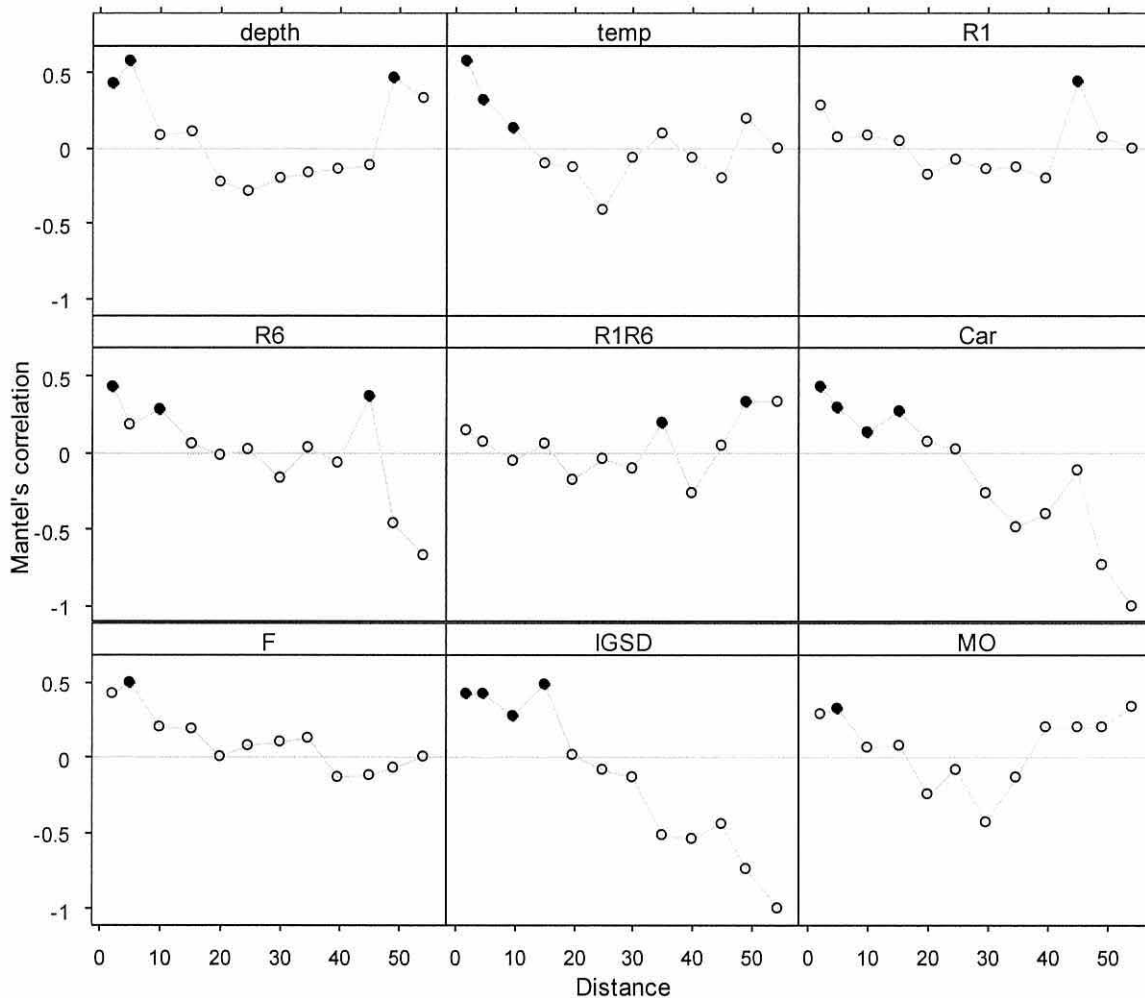
VII-5. DISCUSSION

Simple and partial Mantel tests were able to detect the occurrence of spatial structure in density and biomass of *L. depurator*, as well as in density/biomass residual weights and in sediment variables, even when the effect of depth was eliminated from the relationship. However, the performance of a Mantel test to check the occurrence of a significant spatial structure, was non–conclusive for all variables, since some sediment variables (R1 and φ) were not significantly spatially correlated according to this test, but presented clearly structured variograms (fitted with a spherical and gaussian model, respectively). The inability to detect the spatial correlation in these cases may be due to the lower number of samples (36 samples) or may point to the low statistical power of the Mantel test.

Automatic, semiautomatic or manual variogram model selection has been the subject of much discussion in the literature (Cressie, 1991; Petitgas, 1996; Rivoirard et al., 2000). In this study the minimising function from weighted least squares was used to select the most appropriate spatial model, although previous information on the ecology of the species was also fundamental.

Depth is known to play a key role in delimiting L. depurator populations (Abelló, 1993; Abelló et al., 1988; Mori & Zunino, 1987). González-Gurriarán et al. (1993) considered that although depth may be the major large-scale physical factor affecting distribution patterns, it did not appear to be a determinant within their study area (the Galician coast). This was not the case in the present study, where depth significantly influenced the distribution of the crab. González-Gurriarán et al. (1993) concluded that sediment type and oceanographic conditions were also delimiting the distribution of the species. Previous geostatistical studies with other species also showed depth as a clear delimiting factor (Simard et al., 1992; Sullivan, 1991). The variograms for density, biomass and residual weights were all fitted to spherical model, which showed the smallest residuals (minimising function), as obtained in previous crustacean studies (Freire et al., 1991c; González-Gurriarán et al., 1993; Maynou et al., 1998). Taking into account a depth trend clearly increased the precision of the model.

Previous studies of L. depurator spatial structure on the Atlantic continental shelf (Galicia) detected patch sizes between 14 and 22 km (González-Gurriarán et al., 1993), which is in accordance with present results (between 11 and 21 km, see Table VII-2). Still, also in Galicia, a range of 3 km was estimated inside the Ria de Ferrol (Freire et al., 1993), a much smaller value than that observed in the adjacent Galician continental shelf (González-Gurriarán et al., 1993) and in the present study. These differences may be related with the fact that the Ria de Ferrol sampling area was approximately 15 × 2 km, and the maximum variogram distance was 8 km. It would therefore not be possible to detect a greater patch size in that study (Freire et al., 1993). Results from the geostatistical study performed in the southwestern Adriatic Sea (Ungaro et al., 1999b) detected a patch size (effective range) of 160 km in the spring. This is much larger than the patch sizes observed either in the current study or in the Galician study (González-Gurriarán et al., 1993). However, these authors did not provide sufficient details in terms of distance between samples or variogram maximum distance in their publication to allow interpretation of such large values.

Within the present study area, both density and biomass of L. depurator were higher in the north than in the south. The north is characterised by a narrow shelf (8-10 km width) and a gentle slope cut by deep submarine canyons. In contrast, the southern shelf becomes progres-

sively wider (38-40 km) and the slope steeper. Submarine canyons tend to have high macrofaunal and meiofaunal biomass, related to the higher rates of production and sedimentation from the shelf (Cartes *et al.*, 1994; Maynou *et al.*, 1996). The higher densities of *L. depurator* in the northern area may accordingly be related to an increase in prey resources given the vicinity of the submarine canyons, but further investigations are required to clarify this hypothesis.

The residual weights were a useful, if complex, indication of size distribution. Its use may prove particularly valuable when low number in the samples precludes a full size-frequency analysis. The use of residuals weights successfully discriminated between areas of predominantly large or small crabs, with smaller crabs occupying shallower waters preferentially. Abelló *et al.* (1993) shows a tendency for small *L. depurator* to be found in shallower waters.

Sediment characteristics have been found to delimit the occurrence and distribution of many benthic decapod crustaceans (several species: Atkinson & Taylor, 1988; *Chionoecetes opilio*: Comeau *et al.*, 1998; *Areneus cribarius*: Pinheiro *et al.*, 1996). *L. depurator* distribution characteristics were found to be significantly affected by most sediment variables considered, particularly by temperature, organic matter content and redox potential, although overall the correlation level is low, thus emphasising the ecological strength and opportunistic behaviour of the species. Density and biomass presented a negative correlation with the sorting coefficient (IGSD) and with the differences between redox potential at 1 and 6 cm off the sediment surface. In relation to IGSD, high densities of *L. depurator* were found in well sorted homogeneous sediments, corresponding to low energy areas. Residuals (e.g. size structure of the population) were significantly correlated with grain size (φ), with larger individuals occurring in finer sediments, while small crabs were preferably found in areas with very fine sand sediments. Minervini *et al.* (1982) showed that distribution of *L. depurator* was mainly related to muddy sediments, in contrast with the congener species *L. vernalis*, which was mainly found in sandy sediments. In the present study, both density and biomass presented significant positive correlations with the redox potential, which indicates that the species favoured well-oxygenated sediments.

PART II. Geometric morphometry methods

VIII. Introduction to geometric morphometrics and a short review

VIII-1. INTRODUCTION TO GEOMETRIC MORPHOMETRICS

Variation in body shape can often reflect ecological and behavioural differences between organisms (Klingenberg *et al.*, 2003). Because of the high density and viscosity of water, body shape limits swimming performance in fish and many other aquatic organisms (Webb, 1984). The range of body shapes exhibited by a particular species is a result of countless evolutionary refinements and thus should accurately reflect a range of ecological, physiological and behavioural influences impinging on individuals. Crustaceans, with their hard exoskeletons, are excellent organisms for studying shape differences in relation to the physical and biological environment.

VIII- 1.1. Historical introduction.

The first known approach to the analysis of shape was done in the fifteenth century, by the German artist Dürer, who invented a system to map the human face and then derive caricatures by distorting portions of the mapping grid. Figure VIII-1 shows how Dürer could cause amusing caricatures by either deforming the grid uniformly (e.g. shearing, Figure VIII-1) or non-uniformly by disproportionate changes in only small areas of the grid.

In 1917 D'Arcy Thompson proposed a method to compare the shapes of different species, where the shape change was illustrated throughout deformation grids (Figure VIII-2 and Figure VIII-3). The driving force behind the shape analysis was a desire to indicate evolutionary trends in closely related species and show how apparently vast differences in shape can be relatively easily explained by differential growth of different parts of the same basic patterns.

Figure VIII-1: Human face drawing manipulation from the painter Albrecht Dürer. Images from http://www.xs4all.nl/~androom/dead/durer.htm;

Albrecht Dürer Initial head:

Non uniform changes:

Shearing

Changes in space between lines:
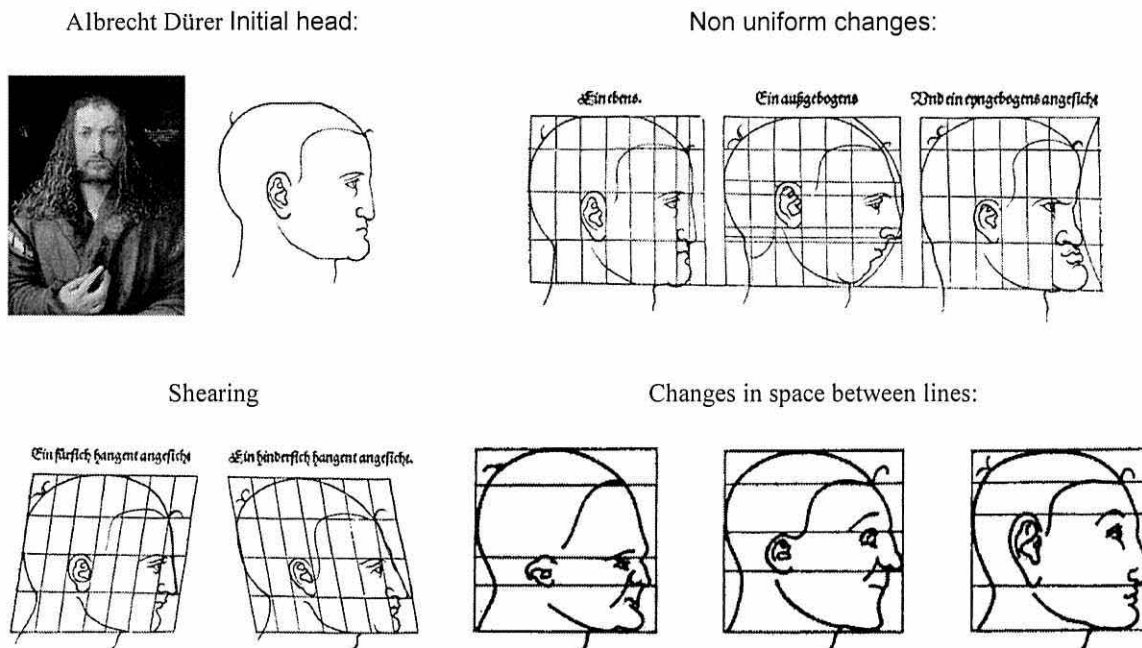
With the onset of rapid computational machines (computers) and the drive towards "numerical taxonomy", traditional morphometric analysis (sensu, Marcus, 1990) and multivariate morphometric analysis (Reyment *et al.*, 1984) has blossomed in the last four decades (Blackith & Reyment, 1971; Jolicoeur, 1963). "Multivariate morphometric" analysis is the application of multivariate statistical techniques to sets of morphological measurements (Adams *et al.*, 2003). Using traditional methods, linear dimensions are measured and analysed alone but multivariate techniques can include, for example spines or teeth numbers, ratios between dimensions or angles intersecting dimensions (Adams *et al.*, 2003). Covariation in the morphological measurements can be quantified, and patterns of variation within and between samples identified (Adams *et al.*, 2003). Statistical analyses typically included principal components analysis (PCA), factor analysis, canonical variate analysis (CVA) and discriminant functions (LDA). Many studies strived to find allometry by studying relative growth differences which lead to changes in shape with increase in size (Jolicoeur, 1963). Because linear distance measurements are obviously highly correlated with general "size" (Bookstein, 1985), much effort was spent developing methods for size correction, so that size-free shape could be extracted and patterns of shape variation elucidated (e.g., Jungers *et al.*, 1995; Lombarte & Castellón, 1990). In many instances, such a size correction is not needed because multivariate techniques tend to find "size" as a major component of the data variability and

often remove it as the 1st principal component or canonical axis, leaving the other ordination axes "size free".

Figure VIII-2: First Fig.: Photograph of D'Arcy Thompson. Other Fig.s: Examples of D'Arcy Thompson deformation grids on fish and skull. Images from http://science.nasa.gov/newhome/headlines/ast28may99_1.htm, http://www.blackwellpublishing.com/ridley/a-z/DArcy_Thompsons_transformations.asp, http://fugu.hgmp.mrc.ac.uk/PFW/Articles/Kunkel/

D'Arcy Thompson

Grid shear:
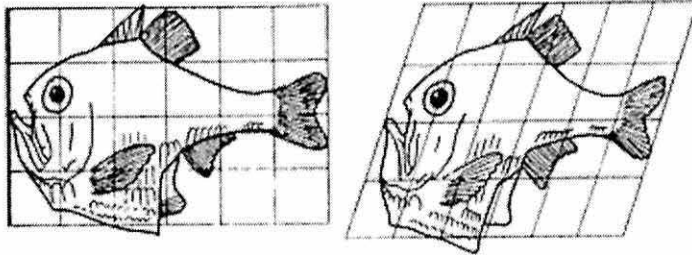
Cirular grid deformation:
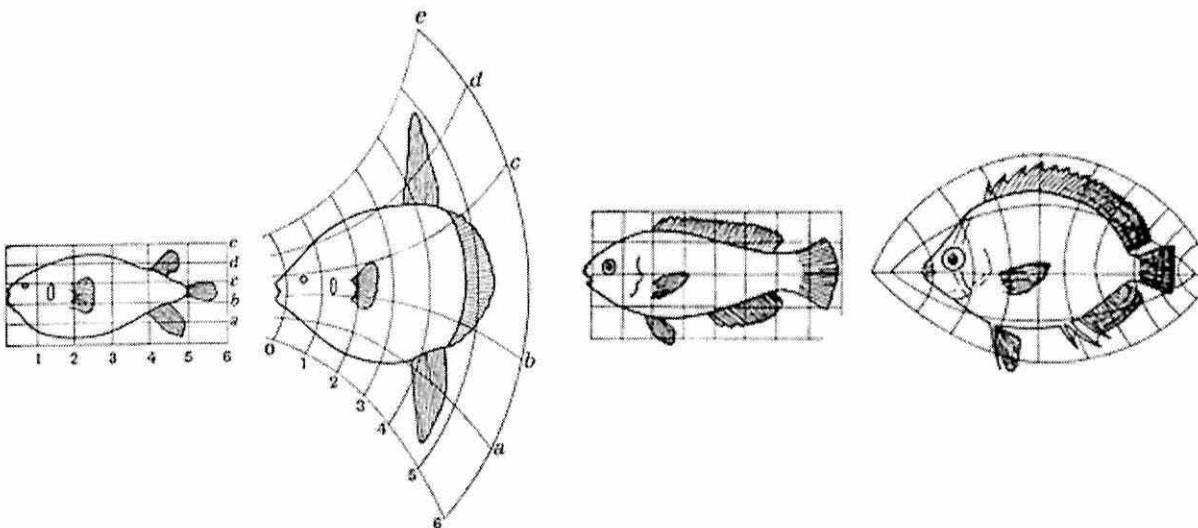
Perspective grid deformations:
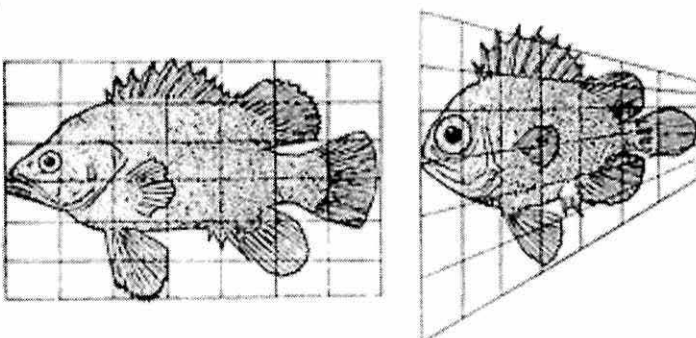
Exotic grid deformations:
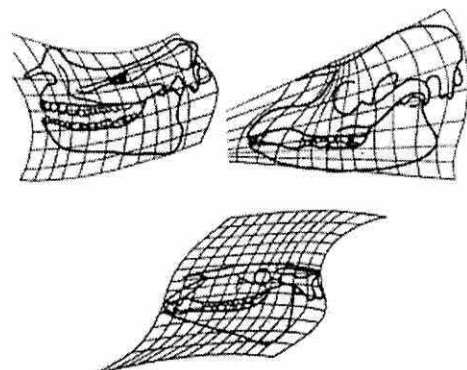
Figure VIII-3: Left Fig.: D'Arcy Thompson deformation grids. Right Fig.: Modern thin-plate spline of a similar example from D'Arcy Thompson. Note that the basic ideas from D'Arcy Thompson are applied currently due to the development of computers, it was not possible before. Images from http://science.nasa.gov/newhome/headlines/ast28may99_1.htm

Skulls of a human, a chimpanzee and a baboon and transformations between them
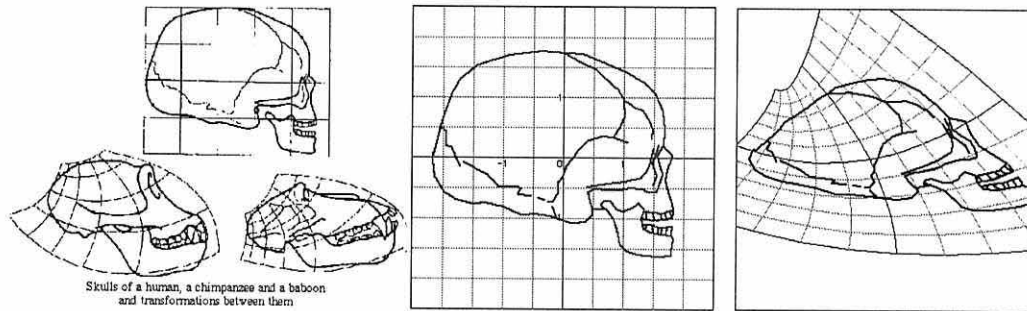
While multivariate morphometrics combined multivariate statistics and quantitative morphology, several difficulties remained. First, many methods of size correction have been proposed, but there was little agreement on which method was the most appropriate. Different "size" correction methods usually yield slightly different results, making comparability difficult. It was also difficult to decide whether "slightly different" was in any way biologically significant. Second, the homology of linear distances was difficult to assess, because many distances (e.g., maximum width) were not defined by homologous points. Third, the same set of distance measures could be obtained from two different shapes because the location of where the distances were made relative to one another was not included in the data. For instance, if maximum length and maximum width were measured on both an oval and a tear-drop, both objects could have the same height and width values, yet they are clearly different in shape (Figure VIII-4). Therefore, one expects the statistical power for distinguishing shapes to be much lower than it should be. Finally, it is not usually possible to generate good graphical representations of shape from a few linear distances, shape is certaintly more complex.

Figure VIII-4: Example of two objects (a and b) with the same linear measures (width and height) but different shapes.
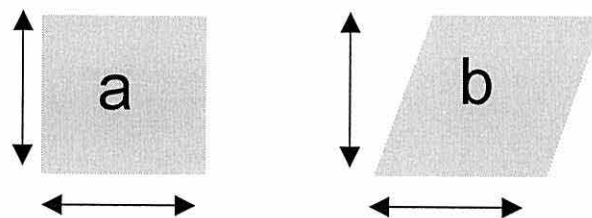
Douglas *et al.* (2001), suggested that three main 'revolutions' in development of (mor-phometric) shape analysis methodologies have occurred. The first was an improvement in shape quantification, with non-orthogonal distances being combined with horizontal/vertical

distances, which basically positions each measurement point through triangulation relative to other points (so called truss based methods, see Figure VIII-5)(Beddow & Ross, 1996, comparison of trusses and conventional measures; Strauss & Bookstein, 1982). The second was an analytical refinement in the quantification of body size and shape, which permitted each to be analysed separately (Bookstein, 1989; Rohlf & Bookstein, 1987). The third, initially adopted by D'Arcy Thompson (1917), graphically, but now made mathematically possible thanks to computing power, is based on relative positions of body "landmarks" or contours on a mapped grid and termed 'geometric morphometric analysis' (GMA). Concurrent with conceptual advances, Kendall (1977) and others developed a more rigorous statistical theory for shape analysis employing multivariate statistical methods for considering numerous "shape" measurements simultaneously (Adams *et al.*, 2003). Increased computing power also allowed direct visualisation of the shape (and changes thereof) from the dimension measurements landmark distributions.

Figure VIII-5: Example of a truss network using 11 landmarks (from Palma & Andrade, 2002).
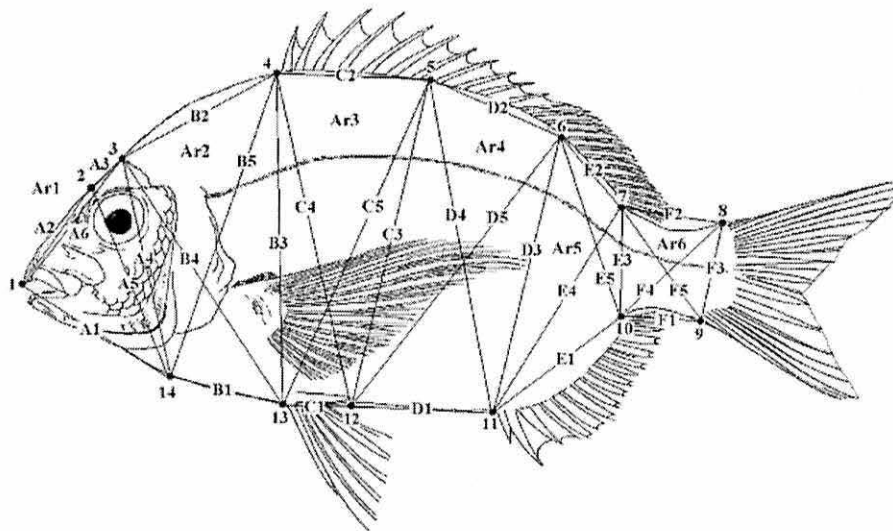
Geometric morphometric approaches require or produce (Bookstein, 1985; Rohlf, 1990; Rohlf & Marcus, 1993; Zelditch *et al.*, 1998):

1. The exact definition of anatomical homologies, so that landmarks can be consistently identified on any specimen.

2. The quantification of landmarks without distorting shape and from that the production of potential shape variables for analysis by multivariate techniques to elucidate differences

3. Deformation grids to visualise shape differences between different forms on a landmark-by-landmark basis.

VIII- 1.2. Why use geometric morphometry?

Geometric morphometry can describe and locate differences of form in organisms more efficiently than can multivariate analysis of traditional distances measurements, even when the distance measurements form a truss grid (Bookstein, 1991). The GMA approach has yielded rewarding information in fish eco-morphological studies (Walker, 1997).

Douglas *et al.* (2001) observed similar results between trusses and landmark-based methods. Both Walker (1997) and Douglas *et al.* (2001) provided a visual demonstration of phenotypic differences between fish species and populations within species, which led directly to a re-appraisal of species management policies (Douglas *et al.*, 2001).

VIII- 1.3. What is geometric morphometry?

"It is important that users of these methods appreciate the relationship between theoretical aspects of GM and their practical application" (from Slice, 2001).

The objective of the current section is to give an introduction to the techniques of geometric morphometry. A summary of the main steps of analysis are given in Figure VIII-6.

Landmarks

In geometric morphometry, the first step is to define the landmarks. Landmarks are chosen on an object/specimen which are homologous between different objects or specimens. For example the end of the rostrum on Crustacea having a rostrum, the middle of the eye or the top of the operculum on teleost fish (e.g. Figure VIII-7), can be chosen for landmarks as long as they are equivalent locations between objects to be compared. Choosing landmarks is essentially a preliminary analysis, because landmarks must reflect the shape of and potential shape changes in the objects being analysed otherwise GM analysis is unlikely to show anything. The choice of landmarks must have biological meaning and should be carefully chosen to highlight differences between specimens, within and between species.

There is no limit (upper or lower) to the number of landmarks used to define each specimen, common sense dictates that 2-3 will be too few and using every point on a digitised image must lead to considerably redundancy and inefficiency. Rolhf (pers. com.) advises the use of at least twice as many specimens as landmarks per group being analysed. Marcus *et al.* (1996) recommend three or even four times the number of specimens as landmarks being analysed for an adequate analysis. The greater the number of landmarks, the greater is the

number of shape variables that can be found to define the object and so, theoretically, the better will be the description of the shape. With a large number of variables to be analysed a large number of replicates will also be necessary to maintain the statistical power of any test of difference applied. However, some landmarks may not be informative, and so it may prove more efficient to the analysis, hence potentially increase the statistical power. Preliminary observations with a few specimens, are often helpful in establishing the potential shape differences, and hence determine the most relevant landmarks for the study.

Figure VIII-6: Summary of the main steps to be performed in completing a geometric morphometric analysis. Examples of a freely available computer software to perform each task are given in Box 1 and 2. Key concepts are highlighted in bold and darks grey boxes indicate 'actions'. ❶❷❸❹❺❻ are referred in the text throughout the document.
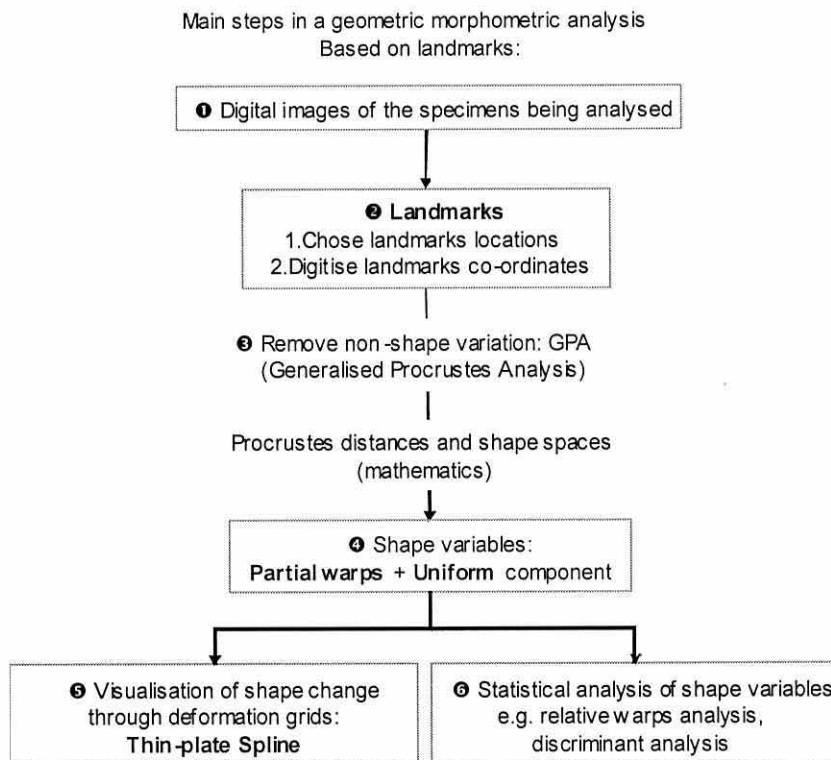
Figure VIII-7: The arrows with the numbers indicate examples of landmark location (from Loy *et al.*, 2001)
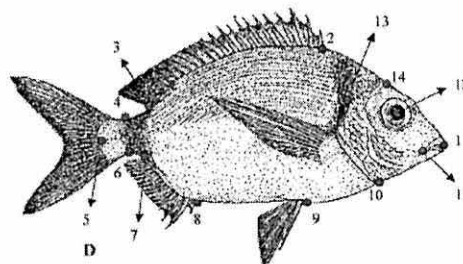
Mindful of landmark choice criteria, Bookstein (1985), defines three types of landmarks (see Figure VIII-8):

Type I (true landmarks). These are interspecific and homologous structures based on the strongest, usually histological and ontogenetic evidence e.g. position of eyes, mouth, anus, skeletal parts, spines.

Type II (pseudo-landmarks). These represent the limits of clearly defined structures, or the point of the maximum curvature, inflexion, ... They are the geometric extensions and de-limitation of homologous structures.

Type III (relative landmarks). These are relative measures of the same homologous object, e.g. the points of maximum length or width of a crab carapace. Type III landmarks usu-ally characterise more than one structure. The multivariate machinery of geometric mor-phometry can use type III landmarks but they are usually less defined (hence more variable) than type I or II landmarks and present more difficulties in interpretation, especially in com-parisons between species (Slice *et al.*, 1996).

Figure VIII-8: Examples and illustration of landmark's types.
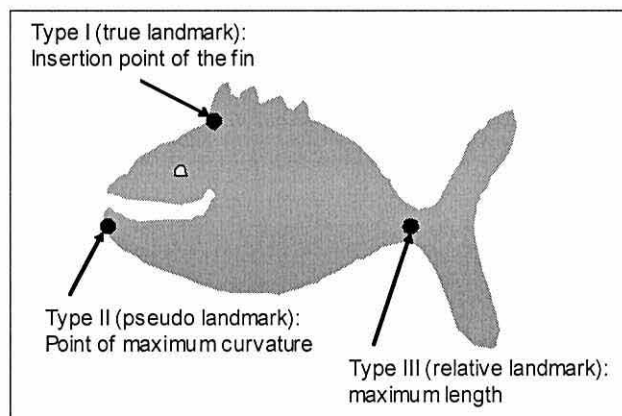
Direct analysis of landmark co-ordinates as variables would incorporate the variable ef-fects of orientation and general 'size' of the specimens thus obscuring any shape differences (Adams *et al.*, 2003). Therefore, the variation, which is not attributable to shape, must be mathematically removed prior to the analysis. Once distortion due to orientation and 'size' has been eliminated from the landmark co-ordinates, they can be considered "shape vari-ables". These variables may then be compared unambiguously between samples and unbiased graphical representations of the general shape may be readily generated (Adams *et al.*, 2003).

Removal of non-shape variation: Generalised Procrustes Analysis (GPA)

Generalised Procrustes analysis (GPA: also called generalised least squares, GLS) adjusts landmark co-ordinates to the orientation and 'size' (assuming isometry throughout) for each species by using least-squares estimates for how far each landmark for each specimen image is spatially moved or rotated due to image orientation and 'size' distortion. Initially, the centroid (generally the geometric centre of gravity for that particular set of landmarks but any sensible "centroid" can be defined if it is homologous between specimens e.g. the centre of an eye) of each landmark configuration (i.e. specimen shape) is redesignated as co-ordinate 0,0 (Figure VIII-9), thus standardising the co-ordinate system for each set of landmarks. The landmark co-ordinates are then optimally rotated to minimise the squared differences between corresponding landmarks from different specimens, by successively minimising the distances between landmark 1 for all specimens, then landmark 2, etc. Finally, landmark co-ordinates are then scaled to unit size by dividing each by centroid 'size'. Centroid 'size' is defined as the square root of the summed, squared distances of all the landmarks from the geometric centroid and is used as an appropriate measure of overall body size since it is un-correlated with shape (Rohlf & Slice, 1990) (Figure VIII-9 and Figure VIII-10; see Box 2 for examples of available software).

Box 1.

The first step in a geometric morphometry analysis is to digitise the specimens that are being analysed (Figure VIII-6 ❶). This can be done through the use of a digital (or not) photographic camera, high-resolution scanner or a digitising table.

Once the specimen's images are available in the computer and the landmark positions determined, it is necessary to locate each landmark in all specimens. The co-ordinates of the landmarks are than saved in a file for latter analysis (Figure VIII-6 ❷). All these can be done using tpsDig (tps series freely available in the internet)(Rohlf, 2003a). For creating the images file, tpsUtil can be used, otherwise any text editor can be used.

Figure VIII-9: Main steps in Procrustes Superimposition Analysis (GPA).
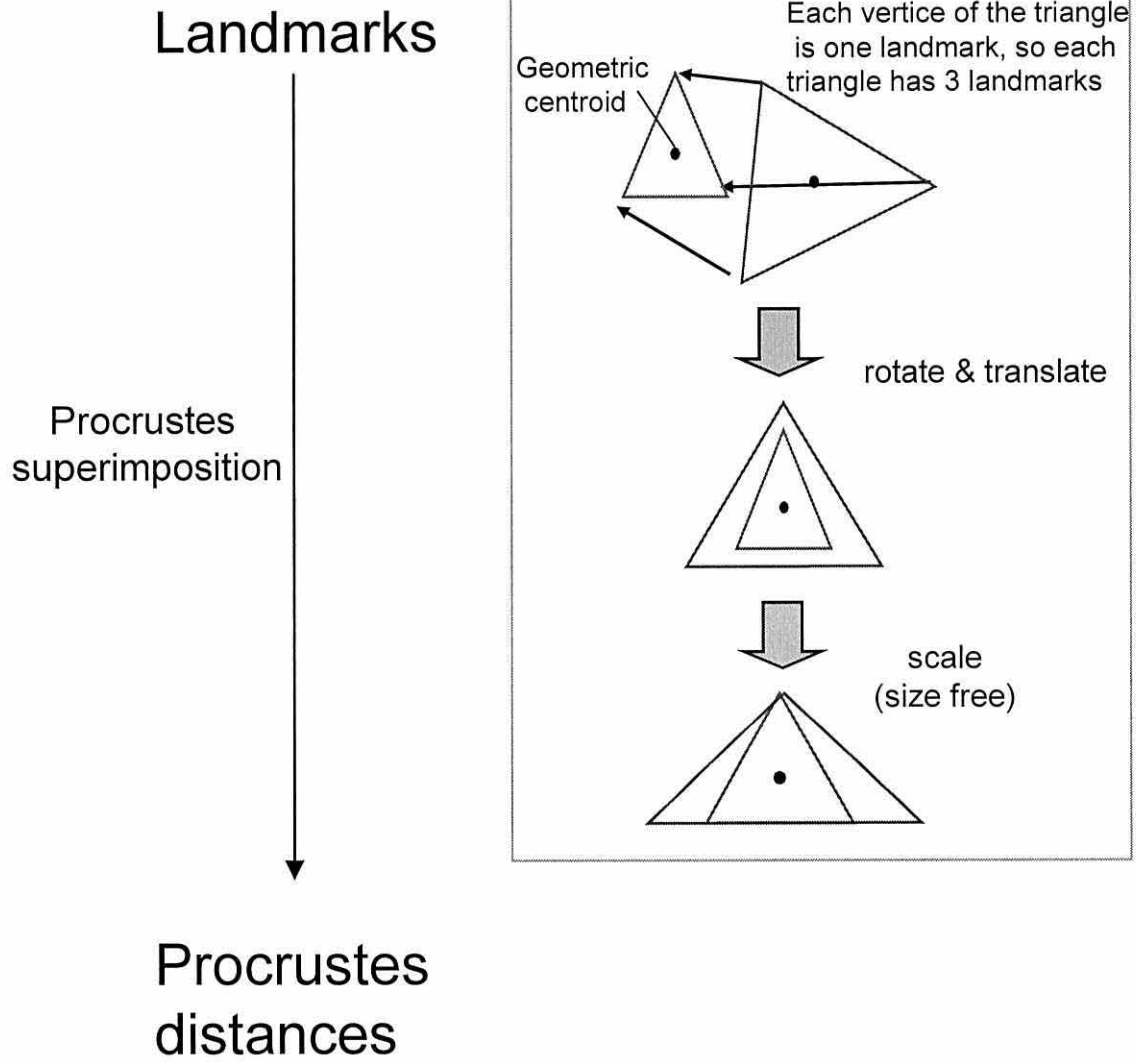
Figure VIII-10: Example of the main steps in Procrustes Superimposition Analysis (GPA), in an analysis of 30 specimens (15 males and 15 females) of the portunid crab *Bathynectes maravigna* carapace shape. (a) landmarks in the crab's carapace (left figure) and the co-ordinates of these (right figure). (b) From left to right, translation, rotation and scaling of the landmarks co-ordinates. (c) after GPA, align specimens.
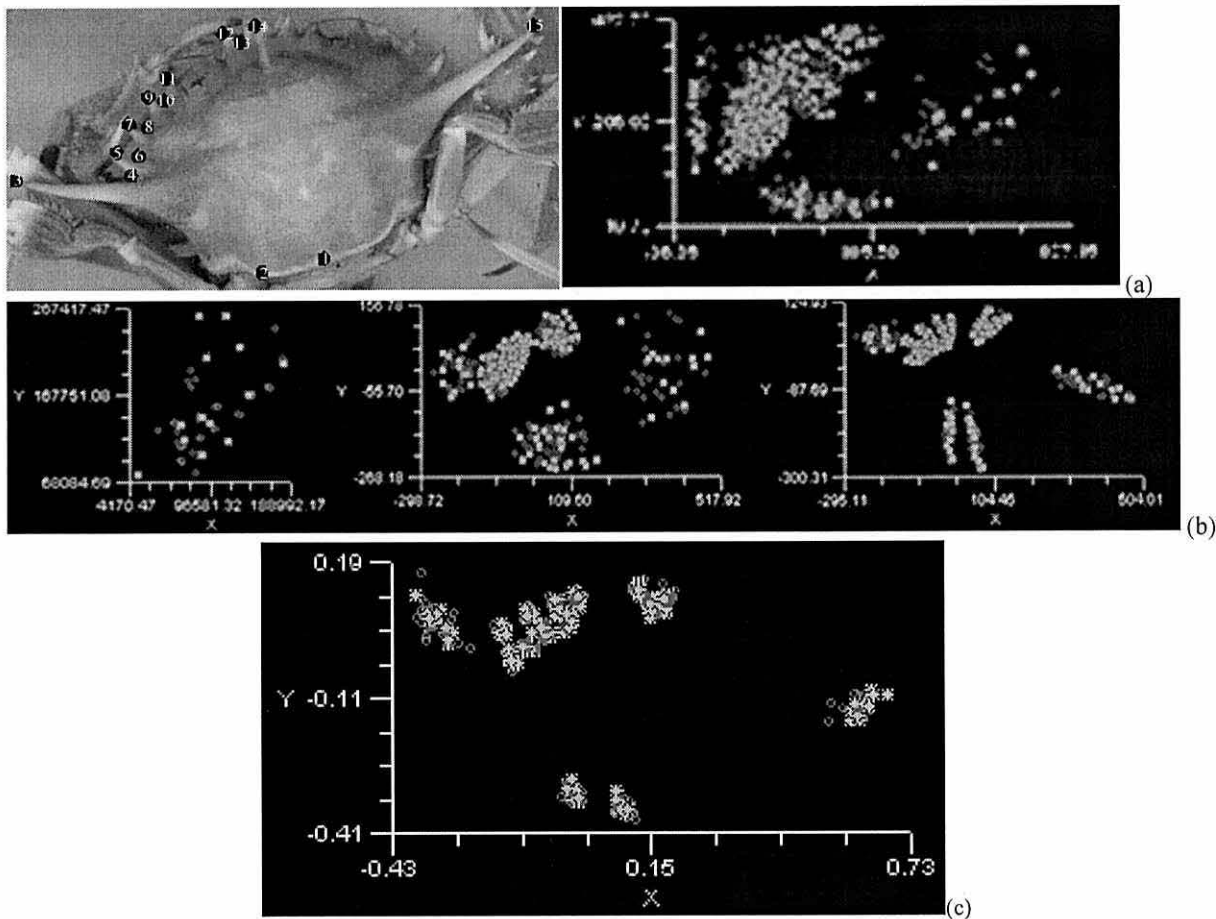
When variations in shape are shown only by a small proportion of the chosen landmarks, GPA is apt to produce an artefact known as the "Pinocchio effect"[1] (Rohlf *pers. com.*). Using GPA the large differences in position of one or two landmarks gets redistributed throughout and diluted by the small differences in the remaining landmarks. Walker (2000) showed how shape differences in *Gomphosus varius* were not well modelled using GPA techniques (see Figure VIII-11) but were readily identified using a generalised resistant-fit (GRF), which avoided the 'Pinocchio effect' (Rohlf & Slice, 1990; Slice, 1996). However, in contrast to the use of GPA, GRF techniques cannot be used in further statistical analyses (because the algebra underlying the Procrustes fit is a least squares approach), but are useful in the visualisation of shape change (Rohlf & Slice, 1990).

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1 The 'Pinocchio effect' is named so because it implies that the GPS would not have been able to detect the large nose on Pinocchio (when comparing him with another child) and would have distributed the difference in the nose of Pinocchio and another child throughout all the remaining landmarks. In contrast with GRF, is expected to correctly identify the Pinocchio nose large as it was.

Figure VIII-11: Example of the 'Pinocchio' effect. (a) *Gomphosus varius* small and large individuals (from Walker, 2000). (b) differences between two groups of individuals using GPA(c), and using GRF (d). Note that the vectors indicate the 'amount' of shape difference from the consensus to (a) multiplied by 3 for a better visualisation. Note the difference in landmark five.

(a) Small individuals

(b) Large individuals

(c) Difference between specimens using GPA

(d) Difference between specimens using GRF
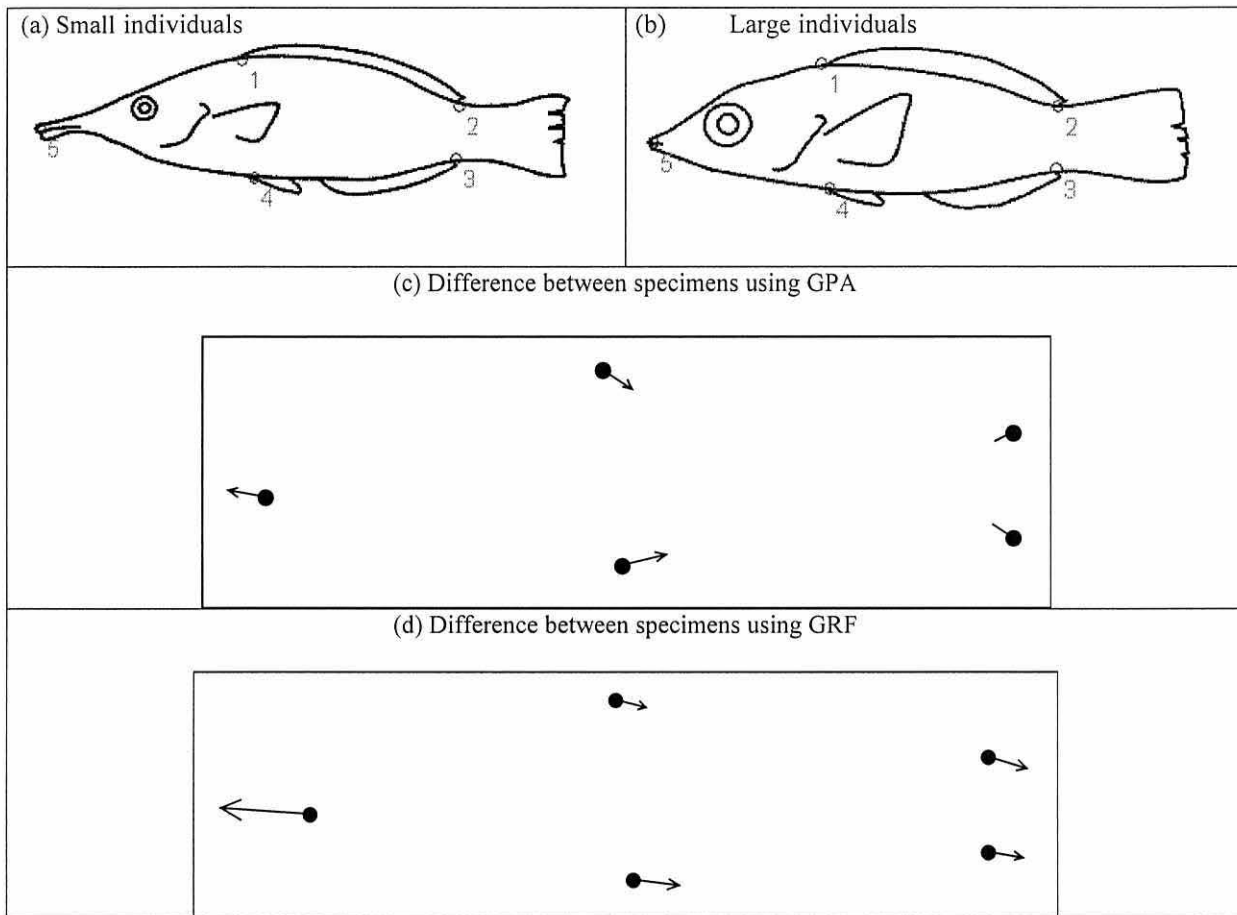
Procrustes distances, Kendal's shape space

With co-ordinates scaled and oriented (called 'superimposition'), shape differences can be described by the differences in co-ordinates of corresponding landmarks between specimens. Often such differences have been analysed by multivariate ordinations of shape variation (see Rohlf, 2000a).

Additionally, the aligned specimens from GPA provide points that can be projected into a space that is tangential to Kendall's shape space (see Rohlf (1999) and Rohlf (2000a) for details and discussions on tangent spaces in morphometrics)(Figure VIII-12). In this linear tangent space, distances between pairs of points (specimens) approximate the Procrustes distances (the square root of the sum of the squared differences between the landmark and the consensus or average configuration) between the corresponding pairs of landmark configurations. Procrustes distances are an absolute measure of the degree of shape difference between two configurations (Rohlf, 2000a).

Kendall (1977) developed the concept of "sets" of shapes as occupying "shape space" and individual shapes being represented by points within that space. For simple three cornered shapes (triangles) the "shape space" is mathematically equivalent to a sphere with any point on the surface of the sphere representing a differently shaped triangle. More complex shapes occupy more complex configurations with that for a four cornered shape resembling a doughnut (Goodall, 1991). The angle (in radians) of each shape point, in its respective shape space, to the mass centre of the space is the so called "procrustes" distance which defines the shape after transformation of the shape to account for orientation and scaling. The geometry of even simple shape spaces is decidedly non-Euclidean hence not amenable (except in rare circumstances) to standard statistical techniques which utilise Euclidean distances between measurements. When the positions of the shapes are normally projected (i.e. at right angles) onto a plane which is tangential to the shape space in the vicinity of the (usually) clustered shape points, approximate "procrustes" distances can assume Euclidean co-ordinates (within the "tangent space") which are amenable to standard statistical techniques. With the usual array of limitations, it is then possible to attempt statistical separation of groups of similar shapes, one of the main aims of geometric morphometry. Figure VIII-12 attempts to conceptualise the procedures for deriving these Euclidean co-ordinates for a simple (triangular) shape using a process equivalent to warping the shape space to a flat plane (Adams *et al.*, 2003, and ref. therein).

Thus, the shape deformation can be decomposed into two components: uniform (affine) and non-uniform (non-affine, which is represented by the partial warps). The uniform component describes changes that are of the same magnitude and direction of the whole organism. The non-uniform shape change describes local differences in the landmarks which represent transformations that differ over body regions. So, each landmark may have diverse directions and scales of shape change (Reis *et al.*, 1998). The uniform component and the partial warps can be treated together or separatly in a multivariate analysis. However, it is not possible to analyse or interpret the partial warps separately since they act together in ascribing position to the projected shape in shape space (Adams & Rosenberg, 1998) (see Box 2 for examples of available software).

Figure VIII-12: Projection of a triangle in Kendall's space. The dot indicates the location of the triangle in the sphere. U1 and U2 are the uniform components. The Procrustes distances are within the spherical Kendall's shape space, and are projected into the tangent space. The projections of the Procrustes distances into the tangent space, are the partial warps.

Pre shape space   Shape space   Tangent space

Co-ordinates in the
shape space
(non-euclidean)

Principal Warps

Thin-Plate Spline   →   How much warping of the
shape space is needed,
from the consensus
configuration (reference
configuration) to arrive at
the flat tangent space

Partial Warps:
non-uniform shape change
+
Uniform components:
uniform shape change

Co-ordinates in the
tangent space
(euclidean)

Box 2.

Once the landmark co-ordinates were saved into a file, GPA and can be done (Figure VIII-6 ❸). For doing relative warps analysis tpsRelw can be used (Rohlf, 2003b)(Figure VIII-6 ❹-❺). For doing any multiple regression (including MANOVA) tpsReg (Rohlf, 2000b) can be used (Figure VIII-6 ❹-❺). Both programs allow one to extract the consensus configuration, uniform components and partial warps and to visualise shape changes through thin-plate spline. A visualisation with GRF is also available. Other software (also freely available in the internet) such as Morpheus and IMP can also be used. For doing PLS, the package tpsPLS is available.

For other multivariate analysis, simply export the data (partial warps and uniform component) and use any statistical package. Within the freely available packages the use of R (a clone to s-plus) is recommended (Ihaka & Gentleman, 1996). The 'tps series' was developed by James Rohlf, who also developed the statistical package NTSYS which performs most multivariate analysis recommended by this author and is able to read directly the data files produced within the 'tps series'; however, this package is not free of charge.

Statistical analysis and visualisation of shape differences

The final step of a morphometric analysis is the statistical analysis of differences between groups of shapes, some form of graphical representation of the shape differences and a logical interpretation of the "biological" significance of any differences.

An important strength of geometric morphometry methods is that graphical representations of results in terms of the re-scaled and aligned configurations of landmark points are a natural output of the technique (Adams *et al.*, 2003). The geometry of shape is preserved throughout the analysis (Adams *et al.*, 2003). Typically, shape differences are presented in a manner analogous to D'Arcy Thompson's (1917) transformation grids. The reference shape is normally shown on a rectangular grid with the extremes of shape shown alongside on "deformed" grids indicating where differences in shape from the reference shape (usually the consensus configuration) occur. The grids showing the extremes of shape can be thought of as elastic sheets (or thin plates) which, when stretched or compressed, represent the way in which the reference shape has been deformed to arrive at the extreme shapes.

The parameters of the thin-plate spline describing these deformations (partial warps) applied to individual specimens to produce partial warp scores can be used as shape variables for statistical comparisons of variation in shape within and between populations. However, these shape variables are derived as transformations from non-Euclidean to Euclidean geometries and they define the "total shape" and not particular bits of shape change. Their

statistical analysis must, therefore, be simultaneous and only multivariate techniques, considering the variables together, are applicable[2].

Apart from multivariate techniques for discrimination such as LDA (Linear Discriminant Analysis) and CDA (Canonical Discriminant Analysis), Principal Components Analysis (PCA) of the TPS partial warps has become more common in shape analysis often being referred to as "relative warp analysis".

A recently developed tool for statistical analysis of shape differences is the Two Block Partial Least Squares method (2B-pls, e.g. Rohlf & Corti, 2000), which is used to analyse the covariance between two sets of variables (similar to a canonical correlation analysis). The technique can be used to compare shapes or to see how shapes vary with a set of independently derived variables (e.g. environmental gradients in temperature, humidity, etc). Dean (1999a) applied the technique to study the relationship between head morphology and prey type in the salamander *Plethodon* sp. and Rohlf and Corti (in prep) examined shape differences between the ventral and dorsal views of house mice skulls. Corti *et al.* (1996) examined mandibular shape differences in the mole rat in relation to eco-geographic variables (e.g. temperature, humidity, rainfall, soil type and vegetation)

According to Rohlf & Corti (2000) the fundamental advances in geometric morphometry over the traditional approaches are in the development of powerful, multivariate statistical methods designed almost specifically for the analysis of the shape data.

As with any biological measurements, variability is introduced from numerous sources. Apart from the natural, genetic variability between specimens there is also measurement variability associated with digitising the image, and locating landmarks. There is still no consensus on how these sources of variability can be adequately assessed and quantified in shape analysis. Phillips *et al.* (1984), Arnqvist & Martensson (1998) and Reig (1998), among others, have proposed several alternatives. The "most appropriate" approach is still unclear and is currently a matter of debate. Clearly, if the error associated with the measurement is greater than the difference of interest then we have no ability to discriminate the difference. Simple procedures, of course, can be adopted to minimise measurement error. For example, the order in which images are recorded should be randomised between and within groups of subjects to avoid systematic error. Furthermore, digitising specimen images and the landmark locations should be done with the same, carefully calibrated device that is free from shape distortion, if the image scale is changed (see Box 1. for software details).

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2 This explains why the partial warps should always be interpreted together, as a whole.

VIII- 1.4. General bibliography

A series of workshops has brought geometric morphometry to the attention of biologists and led to the publication of a series of books where the methods have been explained, discussed, developed and tested (for a recent review: Adams *et al.*, 2003; red book: Bookstein, 1985; orange book: Bookstein, 1991; black book: Marcus *et al.*, 1993; white book: Marcus *et al.*, 1996). Most published scientific papers on morphometry provide little detail on the methods so the workshop reports are the basic reference source. The mathematical tools of geometric morphometry are detailed in Bookstein (1991) and Small (1996), with a brief synopsis given by Rohlf & Marcus (1993). An historical introduction is provided by Marcus & Corti (1996) and many updated details of shape statistics can be found in Dryden & Mardia (1998).

VIII- 1.5. Geometric morphometry applications in Marine Biology.

Although the field of geometric morphometry studies is still recent, it is applicable to all areas of science and engineering (Table VIII-1). Within Marine Biology most studies have been done with teleost fish species (see Table VIII-1), although some have been done with molluscs (cephalopods statoliths: Dommergues *et al.*, 2000; mussel shells: Innes & Bates, 1999; clams shells: Palmer *et al.*, In press; gastropods shells: Stone, 1998).

Studies of fish morphology using these techniques have been applied to many areas of research including: aquaculture (e.g. Corti *et al.*, 1988; Loy, 2000; Loy *et al.*, 1999; Sará *et al.*, 1999), evolution (e.g. Bookstein, 1985), ecology (e.g. Walker, 1997), ontogeny (e.g. Reis *et al.*, 1998), allometry (e.g. Loy *et al.*, 2001; Loy *et al.*, 1998) and internal anatomy (e.g. Loy, 2000) (Table VIII-1).

Table VIII-1 presents a summary of published studies using geometric morphometry, by application, methodology and comparison.

Crustaceans should be a suitable group for the application of geometric morphometry, due to their hard exoskeleton and easily identifiable, homologous landmarks. However, the application of geometric morphometrics to studies of crustaceans has been, so far, limited to the works of Rosenberg (1997; 2002) and Cadrin (2000; 1999).

Table VIII-1: Examples of geometric morphometrics (GM) applications in marine biology studies.

Area of application	Animals	Ref.
Area of application		
Comparison of wild and cultivated stocks	Salmon	(Hard *et al.*, 2000)
Growth and rearing condition	Sea bream	(Sará *et al.*, 1999)
Growth and rearing condition (% salinity)	*Dicentrarchus labrax* (sea bass)	(Loy *et al.*, 1996a)
Growth and rearing condition (temperature)	*Cyprinus carpio*	(Loy *et al.*, 1996b)
Internal anatomy	Sea bass	(Loy, 2000)
Cephalopod Statoliths		(Dommergues *et al.*, 2000)
Symmetry studies	*Amphilophus citrinellus* (cichlid fish jaw)	(Klingenberg *et al.*, 2002)
Species differentiation	Cichlid Fish (3 sp)	(Klingenberg *et al.*, 2003)
	Cichlid Fish (2 sp)	(Kassam *et al.*, 2002)
	Redfish (2 sp)	(Valentin *et al.*, 2002)
	Darters (3 sp)	(Guill *et al.*, 2003)
	Cyprinidae (2 sp)	(Douglas *et al.*, 2001)
Phylogeny	Percidae (31 sp)	(Guill *et al.*, 2003)
Ecomorphology	Serranid Fish (6 sp) and feeding habits	(Cavalcanti *et al.*, 1999)
	Stickleback fish and feeding habits	(Walker, 1997)
	Fish (lagoon)	(Neves & Monteiro, 2003)
Feeding ecology	Lethrinidae fish	(Carpenter, 1999)
	Gasterosteus aculeatus (stickleback)	(Caldecutt & Adams, 1998)
Geographic variation	Mullet	(Corti & Crosetti, 1996)
	Cyprinidae (8 sites)	(Douglas *et al.*, 2001)
	Cichlid Fish (8 sites)	(Klingenberg *et al.*, 2003)
Allometry		(Klingenberg, 1998; Klingenberg *et al.*, 2003; Klingenberg & McIntyre, 1998; Loy *et al.*, 1996a; Loy *et al.*, 1998; Reis *et al.*, 1998)
	Ciprinid fish	(Hood & Heins, 2000)
	Callichthys callychthys (ciprinid fish)	(Reis *et al.*, 1998)
	Dicentrarchus labrax (Sea bass)	(Loy *et al.*, 1996a)
Growth	Life history of Salmon	(Letcher, 2003)
Shape relationship with stomach contents	Salamanders	(Adams & Rohlf, 2000)
Methodology:		
Measurement error within GM	Perch	(Arnqvist & Martensson, 1998); (Klingenberg, 1996); (Reig, 1998)
Articulated structures	Salamanders	(Adams, 1999a; Adams, 1999b; Adams & Rohlf, 2000)
Motion GM		(Slice, 1999; Slice, 2002)
Fluctuating asymmetry		(Klingenberg & McIntyre, 1998)
Disparity	Fish	(Zelditch *et al.*, 2003)
Quantitative genetics	Mouse	(Klingenberg & Leamy, 2001; Klingenberg *et al.*, 2001)
Genetic variation and developmental modularity	review	(Klingenberg, 2002)
Heritability of biological shape		(Monteiro *et al.*, 2002)
3D landmarks (Figure VIII-13)	Weasul skull, cats, etc.	(Reig, 1998; Reig *et al.*, 2001)
Automatic landmarks extraction	*Cyprinus carpio*	(Loy *et al.*, 1996b)

(Table VIII-1 cont.)

	Animals	Ref.
Comparing morphometric methods:		
Trusses and landmarks	Cichlids	(Parsons *et al.*, 2003)
Classic, Fourier and landmarks	Acer leafs	(Jensen *et al.*, 2002)
Classic and landmarks	Gastropod shell	(Stone, 1998)
Outline and landmarks	*Diplodus*	(Loy *et al.*, 2000)
Statistical power of different GM methods		(Monteiro *et al.*, 2000; Rohlf, 2000a)
Error and biases of different GM methods		Rohlf, 2003 (pdf?)
Mantel test and Procrustes		(Peres-Neto & Jackson, 2001)

Rosenberg (1997) studied the shape difference between the major and minor chelipeds in the fiddler crab *Uca pugnax* (Smith). The differences observed in the major cheliped were associated with the ability to produce more power on closure and suggest that selection for intra-specific combat effectiveness has played a major role in the evolution of the cheliped shape. The same author studied claw shape variation across the genus *Uca* (Rosenberg, 2002). Cadrin (2000; 1999) applied box-truss methods to discriminate sexes and fisheries stocks of *Homarus americanus* (American lobster) based on maturity size (Cadrin, 1995). The same author reviewed the use of morphometrics for the identification of fisheries stocks (Cadrin, 2000; Cadrin & Friedland, 1999).

Figure VIII-13: Examples of 3D Geometric morphometry in skulls cercopithecid monkeys (Reig, 1998; Reig *et al.*, 2001) and *Homo* (Adams *et al.*, 2003).
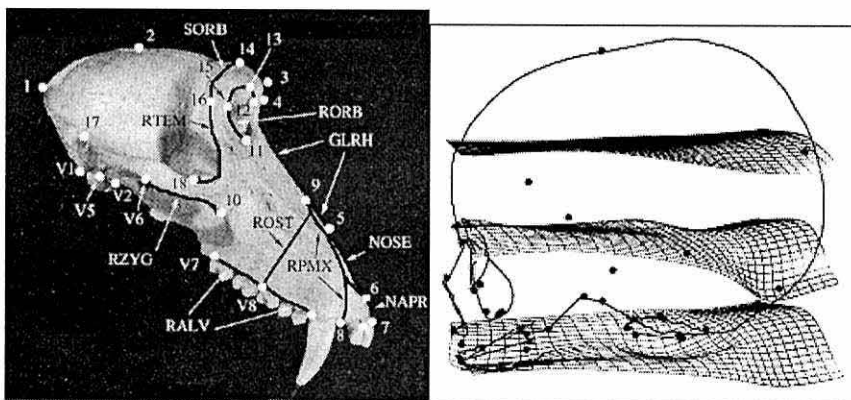
VIII- 1.6. Other methods for shape analysis

Contour analysis

A major limitation of landmark-based geometric morphometry is that a sufficient number of distinctive, homologous landmarks may not be discernible to represent the overall shape (Adams *et al.*, 2003). Thus, there may be large, homogenous areas of a specimen where no

biologically meaningful or precisely locatable points can be identified (e.g. fish otoliths, shells, etc.). Important shape differences may also be located in the regions between landmarks (Adams *et al.*, 2003) (e.g. the lower part of a crab carapace). Figure VIII-14 shows an example of contour analysis applied to bivalve shells.

Figure VIII-14: Example of contour analysis in clams (*Chamelea gallina*) (from Palmer *et al.*, In press).
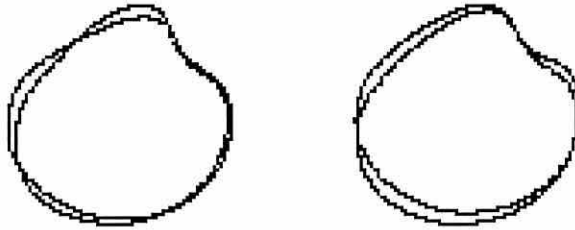
Outline methods were the first geometric, morphometric techniques to be used (Adams *et al.*, 2003; Rohlf & Archie, 1984). While the bounding edge of a structure or region can be considered homologous between specimens, any co-ordinate points used to sample such edges do not necessarily show the same homology. The approach usually used is to digitise points along an outline, fit the points with a mathematical function (usually some form of Fourier transformation), and then compare curves by using the coefficients of the functions as shape variables in multivariate analyses. Points in this multivariate parameter space (e.g., Fourier coefficient space) can be transformed back to the physical space of the organism and visualised as outlines. The approach shows many similarities to landmark-based techniques. The earliest methods fitted lengths of equally-spaced radii from a central point – either a landmark or the mass centre of the object. The technique does not handle major discontinuities (e.g. spines on a crab's carapace) very well and visualises the totality of shape without considering differences in the relative positions of potentially interesting structures (Adams *et al.*, 2003). Furthermore, the statistical power to detect shape differences[3] is much lower than in landmark methods, and so the latter method should be utilised where possible (i.e. if there are homologous landmarks). Thus far contouring methods have been applied to fish otolith shape (Campana & Casselman, 1993; *Hoplostethus atlanticus*, Gauldie & Crampton, 2002; and Gauldie & Jones, 2000; several species, Hamrin *et al.*, 1998; *Merluccius* sp., Lombarte & Castellón, 1990) and shells (*Mytilus* sp., Innes & Bates, 1999; and *Chamelea gallina*, Palmer *et al.*, In press).

Current research is being carried out to overcome the problems of contour analysis for applications where landmarks are difficult to find. Rohlf (pers. com.) is currently developing

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3 Note from the author: using the same specimens, contour analysis was not able to detect significant shape differences between male and female crab carapace, whereas landmark-based methods were.

methods whereby the curve contour between two landmarks (see Figure VIII-15 for an example from human morphology) forms the basis of the analysis. Adams *et al.*, 2003 describe the technique as an extension of the standard procrustes superimposition procedure using a sliding semi-landmark method first proposed by Bookstein (1997).

Figure VIII-15: Analysis of curves. Example of sliding semi-landmarks method applied to modern and archaic humans. Procrustes fits of inner and outer frontal profiles for a) modern humans and b) modern and archaic humans, Australopithecines and chimpanzees using Procrustes analysis of landmarks and semi-landmarks (from Bookstein *et al.*, 2003).
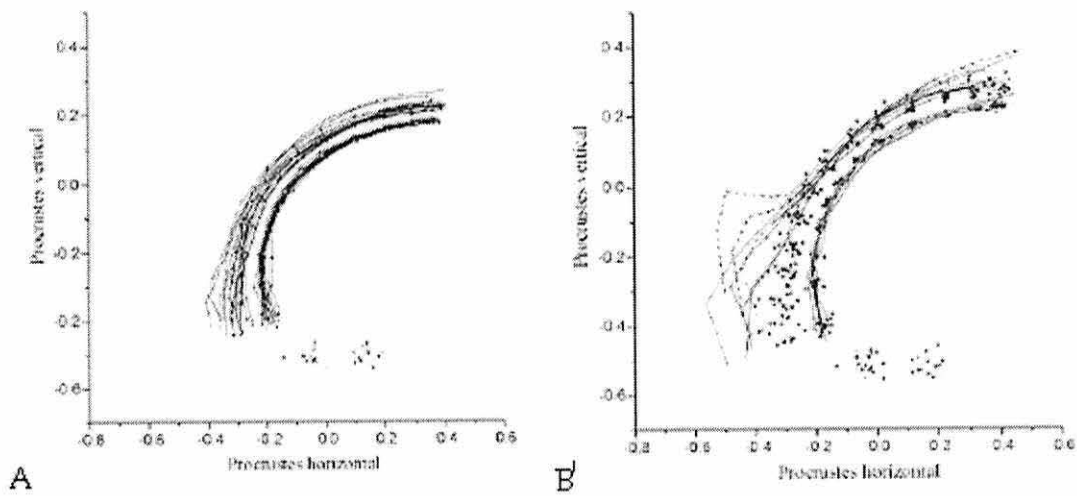
IX. The effect of alcohol and freezing preservation on carapace size and shape in *Liocarcinus depurator* (Crustacea, Brachyura)

IX-1. ABSTRACT

Morphometric and shape analyses are usually performed on preserved specimens. The current paper examines the effect of two common preservation methods, freezing and alcohol, on the shape and magnitude of the crab's carapace. The carapace widths and images of the carapace of two batches of the swimming crab, *Liocarcinus depurator* were taken before and after preservation. The carapace width was measured by two operatives and discrepancy between the two was analysed. The carapace images were analysed using geometric morphometric analysis. The carapace widths decreased significantly, though minimally, after preservation. Geometric morphometry indicated significant differences after preservation in the uniform shape components only, indicating global differences rather than localised differentials.

IX-2. INTRODUCTION

Since crustaceans have hard exoskeletons and potentially numerous "landmarks" they should constitute an ideal group for the application of geometric morphometric methods. Few such studies on Crustacea can, however, be found. Cadrin (1995) applied box-truss methods to discriminate between sexes and potential fishery stocks of the American lobster, *Homarus americanus* (Milne Edwards). Rosenberg's (1997) work on the shape difference between major and minor chelipeds of the fiddler crab *Uca pugnax*, (Smith) probably pioneered the use of landmark-based morphometric analysis in extant crustaceans. The differences observed suggested that the major claw could produce more crushing power, and that selection for "fight effectiveness" may have played an important role in the evolution of the cheliped shape. Rufino *et al.* (2004) used geometrical morphometric techniques to elucidate subtle differences in the carapace shape of male and female *Liocarcinus depurator*.

Recently, reviews of the techniques applied to crustaceans can be found in, Rosenberg (2002, claw shape variation across the genus Uca), Cadrin and Friedland (1999, lobster stock identification) and Cadrin (2000, fisheries stock identification).

In many field studies, individuals are not measured immediately after capture, but are preserved for later measurement. The effect of the preservation on the size of the individuals however significant, is often ignored. The ultimate effect of preservation distortion may

largely depend on the degree of accuracy needed for each specific study. The effect is often quite variable, for example, in many fish species, both adults and larvae, either shrink or enlarge after preservation with alcohol, formaldehyde or freezing (e.g. *Sprattus sprattus*, *Encheylopus cimbrius* and *Pomatoschistus minutus* (Fey, 1999); *Clupea harengus* and *Osmerus eperlanus* (Fey, 2002); *Mullus barbatus* and *M. surmuletus* (Al-Hassan *et al.*, 2000)). The few studies carried out on crustaceans include that of Melville-Smith (2003) who showed that the carapace of the rock lobster (*Panulirus cygnus*) shrank significantly (statistics) after cooking and freezing, although the shrinkage was minimal (numerical). No study has been conducted on the effect of preservation procedure on the over-all shape of the individuals and whether preservation acts in a differential manner on different parts of the body.

Clearly, the interpretation of significant differences in morphometry between species is difficult if the preservation method causes a differential effect between species. Such differential effects of preservatives on different parts of an organism will cause differences in shape, which should be more readily appreciated with geometric morphometry than with any other technique.

The present study examines the effect of different preservation methods on size and shape in the portunid crab *Liocarcinus depurator* (Linnaeus). It is the dominant brachyuran by-catch (untargeted species) in Mediterranean demersal fisheries and shows a wide bathymetric range throughout the continental shelf and upper slope (Abelló *et al.*, 2002; Abelló *et al.*, 1988). *L. depurator* inhabits several types of substrata, although it is most commonly found on mud (Minervini *et al.*, 1982). A wide-ranging species, *L. depurator* has been reported from Mauritania and the Canary Islands to Norway in the eastern North Atlantic and throughout the Mediterranean Sea (d'Udekem d'Acoz, 1999).

IX-3. MATERIALS AND METHODS

Individuals of *Liocarcinus depurator* were collected by trawling off Barcelona (western Mediterranean). The carapace widths (CW) of 120 fresh individuals (60 males and 60 females) were measured by two operatives using the same digital calipers with a resolution of 0.01 mm. The upper view of the carapace was also scanned into a digital image using a calibrated HP Precisionscan 3.1. Thirty male and 30 female crabs, randomly-selected, were frozen (~ −20°C) and the remaining 30 males and females were stored in 70% ethanol. Three weeks later, the frozen crabs were defrosted and the measurements repeated on both groups of crabs.

Landmarks (see Figure IX-1) were used to quantify carapace shape and "Centroid" magnitude (defined as the square root of the summed, squared distance of all landmarks in relation to the geometric centroid (calculated using tpsRel, Rohlf, 2003b) was used as a measure of crab size in addition to CW.

Figure 1 shows the locations of the 15 landmarks identified for the geometrical morphometric analysis. The first landmark was located centrally on the posterior margin of the carapace. The second landmark was the point of maximum curvature of the posterior carapace margin. Landmarks 3 to 11 represent the tips of and anterior notch formed by the five anterolateral teeth. Landmarks 12 to 14 represent the tips of and the notch between the three anterior teeth. Landmark 15 along with landmark 3 delineated the maximum carapace width. Coordinates of the landmarks were digitised using tpsDig (Rohlf, 2003a).

Figure IX-1: Landmarks selected on the *Liocarcinus depurator* carapace.
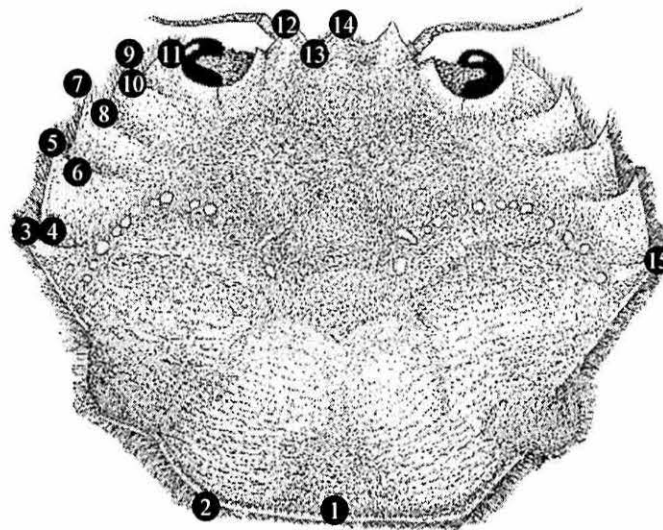
Details on the procedures for geometrical morphometric analysis can be found in Adams *et al.* (2003), nevertheless a brief description is given here. After digitising, landmark maps were rotated, scaled (to unit centroid size) and translated through a Generalised Least squares Superimposition (GLS) procedure (generalised procrustes) to eliminate scale and orientation distorsions ('*tpsRel*' (Rohlf, 2003b)). A thin-splate spline procedure was used to fit an interpolated function to an average map (consensus configuration) of the carapace shape and derive the uniform and non-uniform (partial warps) components of shape variation. The two uniform components describe differences that affect all parts of the carapace equally (global differences). The magnitude of the first of these indicates the degree of stretching along the x-axis relative to the average carapace map, whereas the magnitude of the second indicates compressions or dilatations along the y-axis (Cavalcanti *et al.*, 1999). The non-

uniform shape components (partial warps) describe localised departures from the average carapace map.

The approach followed in the data treatment was to calculate the difference between the operative's measurements before/after conservation, in order to obtain independent samples. A two-sample Wilcoxon test was used to test differences between genders and a one-sample Wilcoxon test, corrected for tied observations was used to test if the CW change due to preservation or operative, was significantly different from zero. Ninety-five percent confidence intervals of the medians were estimated using the Wilcoxon one-sample procedure corrected for tied observations.

IX-4. RESULTS

Carapace width (CW) measurements were not normally distributed and the variances between treatments were not approximately equal. Therefore, differences between operators' measurements and before and after preservation were analysed separately.

Figure IX-2: Box plots of the differences in measurements on individual *L.depurator* carried out by two different operators. * indicate outliers.
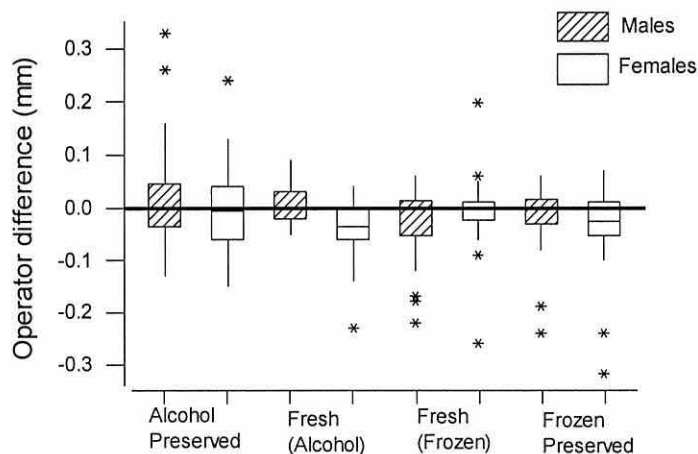
Within the size ranges measured, no significant difference (p>0.05) between measurements on males or females was found (Wilcoxon test corrected for tied observations: W = 7622, p = 0.433) so, in the remaining analyses, both sexes were pooled. There were no significant differences between median differences between operatives across the groups of male and female crabs before or after preservation (Mood's median Test χ = 9.54, df = 7, p = 0.216). Fig 2 shows boxplots of the difference data for each group showing how one or two outliers are evident but that the bulk of the differences were very small. There are no discernible patterns between genders or preservation methods nor between before and after preserva-

tion. The median differences between the measurements made by the two operators was 0.01mm and proved highly significant (Wilcoxon 1-sample test W=7484.5, p<0.001, N=238).

Since the average carapace width was 39.4 mm, a systematic error of 0.025% between operatives is remarkably good, despite the "significance". With such large numbers of observations even tiny and essentially trivial differences tend to become "statistically significant". There was no significant correlation (r = -0.074, df = 236, p = 0.256) between operatives and the size of the crabs, confirming a standard systematic error between operatives which did not vary with crab dimension or applied treatment.

Figure IX-3 shows that centroid size was significantly correlated with CW (r = 0.992, df = 118, p < 0.001).

Figure IX-3: Relationship between carapace width (measured with a digital caliper) and the centroid size (based on 15 landmarks on the crab's carapace) of 120 *Liocarcinus depurator* (60 males and 60 females). centroid = 0.183 + 0.129*CW.
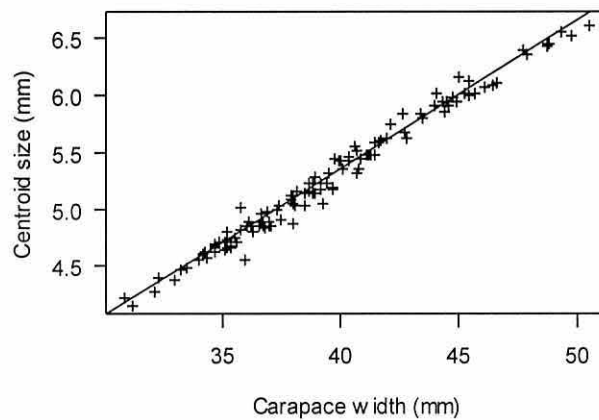
Carapace width decreased significantly (median difference = 0.08 mm) after the animals were preserved in alcohol (Table IX-1), while the centroid magnitude only decreased by 0.01 (median difference not significant, Table IX-1). The effect of freezing was smaller. Centroid magnitude actually increased (median difference = -0.01, Table IX-1), but not significantly. Carapace width, on the other hand decreased significantly (median difference = 0.07-0.05 mm, Table IX-1) after freezing. However, the variability associated with centroid magnitude differences after freezing was far greater than any other treatment

For both the difference in carapace width and in centroid magnitude, with preservation technique there was no significant correlation with the carapace width (i.e. size of the individual), showing no differential effect of preservation technique with crab size.

Table IX-1. Median difference of the carapace width (mm) and centroid size of *Liocarcinus depurator*, between before and after preservation (alcohol or frozen), and respective results of the one-sample Wilcoxon test (V: statistic and p: pvalue).

Preservation	Measure	Operative	Estimated median.	Median	Wilcox	
					V	p-value
Alcohol	CS		0.02	0.01	990	0.065
	CW	A	0.09	0.08	1441	<0.001
		B	0.1	0.08	1709	<0.001
Ice	CS		-0.01	-0.02	806	0.701
	CW	A	0.07	0.06	1423	<0.001
		B	0.05	0.04	1619	<0.001

CS: centroid size, CW: carapace width

Figure IX-4: Median and $\pm CI_{95\%}$ (Wilcoxon), of the difference between conservation methods, on the centroid magnitude and on carapace width of *Liocarcinus depurator* for the two operatives measurements (A and B)
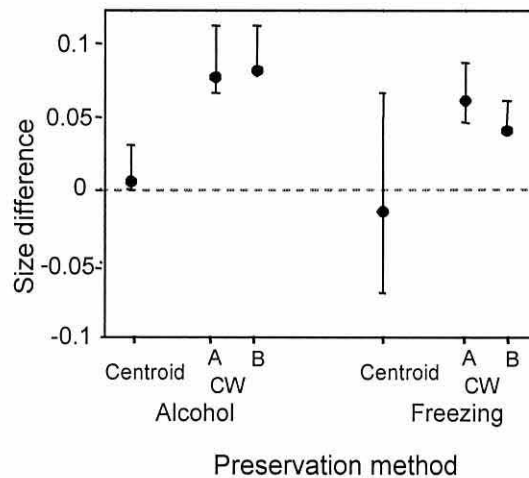
Analysis of the uniform components for crabs preserved in alcohol (Repeated measures MANOVA) indicated a significant effect of the preservation on the shape (Wilks = 0.743, F = 10.016, p <0.001). The resultant discriminant function was not particularly powerful (63% success for pre-preservation crabs and 65% success for post-preservation crabs). Freezing also showed a significant multivariate effect (Wilks = 0.792, F = 7.627, p < 0.001), providing an even less powerful discriminant (58% success for pre-preservation crabs and 60% for post-preservation specimens). Despite determining significant effects of preservation on the global shape parameters, the multivariate analysis could not discriminate well between preserved and fresh crabs simply on the basis of their shape.

The non-uniform shape components exhibited no significant effects of preservation for both alcohol (Manova: Wilks = 0.177; F = 1.415; p = 0.244) and freezing (Manova: Wilks = 0.128; F = 2.082; p = 0.068). Thus, although an overall shrinkage (global change) was evident

in the preserved carapaces such was not reflected in local effects at particular landmark locations.

IX-5. DISCUSSION

Differences in carapace width measurements taken by the two operatives were always smaller than the differences measured between preserved and fresh specimens. The operative effect was shown to be truly systematic and did not vary with treatment or crab size. The precision of each operative was very similar, again emphasising the systematic nature of the difference.

Both alcohol and freezing preservation methods caused significant shrinking of the carapace *L. depurator*. Shrinking by alcohol preservation was slightly greater than that caused by freezing. 70% ethanol is well known for removing water from immersed specimens and presumably does so quicker than exposure to –20 °C which can also create dehydration but usually only under a vacuum.

The individuals of *Liocarcinus depurator* studied ranged from 30.69 mm to 50.53 mm CW. A maximal shrinkage of 100 μm, represents a mere 0.33 to 0.20% decrease, which in practice is relatively trivial. Melville-Smith (2003) also found shrinkage of the carapace after freezing in the *Panulirus cygnus* (rock lobster). Remarkably, given the severity of the treatment, Ibbot (2001) found no effect of boiling and subsequent freezing on the carapace length of *Jasus edwardsii* (southern rock lobster).

Centroid magnitude showed no significant differences due to the different preservation methods, and seemed the most variable of the two measures, particularly for crabs that had been frozen. The inability of centroid magnitude to reflect the obvious differences in CW measured indicates its limitations as a general indicator of 'size'. It must, ultimately, be more variable than a single easily identifiable measure since it is composed of many, often imprecisely located, measures. In the present instance, the variability associated with centroid magnitude hid the significance of the obvious shrinkage and even resulted in the opposite effect being identified (although not significant).

Geometrical morphometric analysis indicated that the effect of preservation on crab shape was significant only in the uniform shape component. All differences in shape were global. Despite the significance, the discriminating power of the derived function was low. The potential for the technique to address tiny differences like those inflicted on the crab carapace by preservation appears limited at present. The errors in digitising, establishing landmark locations and then interpolating the shape functions are clearly greater than the difference revealed by precise measurements of a single, but easily identifiable dimension. In-

creasing the precision of the geometrical morphometric techniques to rival simple measures of 'size' in discriminating power must be an urgent aim. The power to analyse shape as an over-all phenomenon with the precision of simple measurements will make geometric morphometry extremely valuable.

X. Gender and geographic shape differences in the carapace of *Liocarcinus depurator* (Brachyura: Portunidae) using geometric morphometry and the influence of digitising method.

X-1. ABSTRACT

Although presenting great potential, the application of geometric morphometry to crustaceans is in its infancy. The current work describes the use of geometric morphometry in the study of shape variation of the carapace of the portunid crab *Liocarcinus depurator* along the Mediterranean coast of Spain.

Initially, the differences in shape induced by digitising the carapace with either a digital camera or a flat bed scanner. Carapace shape deduced from the camera images proved quite different to those of the scanner images were investigated. This difference was greater than any shape variation due to crab gender or sample location.

Carapace shape was analysed, using MANCOVA (with centroid size as a covariate) of the partial warps and uniform components indicating differences between genders and between sample location; however, significant three way interaction implied that such differences were gender and location specific. Landmarks identifying carapace width, carapace length and abdomen width showed greatest variation, hence gender and location differences were further analysed through the interrelationships between these linear measures. Regression analysis of the relationship between abdomen width and the ratio of carapace width to carapace length indicated clear differences between locations but not between genders. Crabs from the Alborán Sea had proportionally wider abdomens than those from Alicante or North Catalonia. The finding may represent a difference between a southern influx of an Atlantic population distinguishable from a more northerly Mediterranean one.

X-2. INTRODUCTION

Liocarcinus depurator (L.) is the dominant brachyuran by-catch of Mediterranean demersal fisheries down to depths of 200 m (Abelló *et al.*, 2002; Abelló *et al.*, 1988). It is an eurythermal temperate species (Christiansen, 1982; Pérès & Picard, 1965) ranging from the continental shelf to 800 m (Abelló *et al.*, 2002). *L. depurator* can be found on several types of substrata, although it is most commonly encountered on mud and detritus filled sands (see section

I). The species is reported in the north Atlantic from Norway to Morocco, and throughout the Mediterranean Sea (Clark, 1986, and ref. therein).

Morphometric studies on *L. depurator* were done in the Catalan Sea (Abelló *et al.*, 1990a), Ría de Arousa (Galicia, Atlantic coast of Spain) (Fernández *et al.*, 1991) and in the Ligurian Sea (Mori & Zunino, 1987), all using linear measurements. Fernández *et al.* (1991) found differences between the relationship width/length of males and females in Ría de Arousa, with females being broader then males, whereas Abelló *et al.* (1990a) did not observed any significant differences attributable to gender. Furthermore, the female maturity size of *L. depurator* was larger in Ría de Arousa then in the Mediterranean (Abelló *et al.*, 1990a; Fernández *et al.*, 1991; Mori & Zunino, 1987). However, although maturity size was larger in the Galician Ría, growth rates were faster and females attained maturity size faster than in the Catalan coast (Abelló *et al.*, 1990a; Fernández *et al.*, 1991). Immature individuals of *Liocarcinus depurator* did not exhibit growth or 'size' differences between sexes, and those differences arise later, with maturity. Males presented higher growth rates than females, which causes a tendency towards greater abundance of males as size increases both in Galicia and in the Mediterranean (Abelló, 1989; Fernández *et al.*, 1991).

Crustaceans have hard exoskeletons, often adorned with obvious spines, which should make them excellent candidates for shape analysis through geometric morphometry. Such studies are, however, rare. Rosenberg (1997) studied the shape difference between the major and minor chelipeds of the fiddler crab *Uca pugnax*. The differences observed in the major claw suggested the ability to produce more crushing power and that selection for combat effectiveness may have played an important role in the shape evolution of the major cheliped. The same author extended the study across the genus *Uca* (Rosenberg, 2002). Cadrin & Friedland (1999) and Cadrin (2000) applied box-truss methods (related to geometric morphometry) to discriminate gender and fishery stocks of the American lobster, *Homarus americanus* based on size at maturity (Cadrin, 1995).

The objective of the current study is to establish any effect of digitising method in geometric morphometric analysis and to analyse shape changes between the carapaces of male and female *Liocarcinus depurator* from different areas of the Mediterranean coast of Spain.

X-3. MATERIAL AND METHODS

A total of 188 *Liocarcinus depurator* (101 males and 87 females) were collected from the Alborán Sea, Alicante and North Catalonia in the Mediterranean and frozen (-20°C) soon after collection. The carapaces of 125 crabs (63 males and 62 females) of a much more limited size

range, were scanned using a calibrated HP Precisionscan 3.1 and a further 63 crabs (38 males and 25 females) were photographed with a SONY digital camera. Sensible carapace landmarks were identified (see Figure IX-1) and used to quantify carapace shape while "Centroid size" (Rohlf, 2003b) was used as a measure of crab 'size'.

Figure IX-1 shows the locations of the 15 carapace landmarks selected (see Rufino *et al.*, in press). The first landmark was located centrally on the posterior margin of the carapace. The second landmark was the point of maximum curvature of the posterior carapace margin. Landmarks 3 to 11 represent the tips of and anterior notch formed by the five anterolateral teeth. Landmarks 12 to 14 represent the tips of and the notch between the three anterior teeth. Landmark 15 along with landmark 3 delineated the maximum carapace width. Coordinates of the landmarks were measured from the digitised carapace images following Rohlf (2003a).

Details of the geometric, morphometric analysis can be found, for example, in Adams *et al.* (2003). After digitising, landmark maps were rotated, scaled (to unit centroid size) and translated through a Generalised Least squares Superimposition (GLS) procedure (generalised procrustes) to eliminate scale and orientation distorsions. A thin-splate spline procedure was used to fit an interpolated function to an average map (consensus configuration) of the carapace shape and derive the uniform and non-uniform (partial warps) components of shape variation. The two uniform components describe differences that affect all parts of the carapace equally (global differences). The non-uniform shape components (partial warps) describe localised departures from the average carapace map.

Relative warp analysis (similar to a principal component analysis, using the partial warps scores and the uniform components) was performed to examine the major trends in shape variation. The analysis clearly established a systematic difference in shape resulting from the digitising technique.

Abdomen width (distance between landmark 1 and 2), total length (distance between landmark 1 and 14) and total width (distance between landmark 3 and 15) were measured on each digitised image. The inter-relationships between these dimensions were then investigated by more traditional techniques and compared between crab gender and geographic location.

X-4. RESULTS

Figure X-1 shows the results of Relative Warp (RW) analysis. The first Relative warp (RW1) explained 50% and the second (RW 2) 12% of the total variability. Figure X-1 shows that the primordial factor causing differences in shape was centroid size and the first RW of all digit-ised images was clearly correlated to centroid size (Figure X-1 d: $r^2 = 0.56$, F=15.254, N=

188, p <0.001). Since size is removed from the analysis by the re-scaling procedure, relative warp one must indicate a continuous difference in shape from smaller to larger crabs.

The size range of crabs digitised with a scanner was greater than the ones digitised with a camera, which were large crabs only. Thus, the shape differences between the two digitising methods are comparable only between larger crabs. On the first relative warp, digitised and scanned images do not differ and the 'size' of the crabs is correctly identified. On the second relative warp, however, the camera and scanned images are clearly separated with those from the camera consistently more negative on the axis (Figure X-1 a). Furthermore, the variability associated with camera image ordinations appears larger than that of equivalent sized scanned images. The shape difference between digitising methods was confirmed as significant (MANOVA: Pillai's lambda=0.27, $F_{(26,161)}$=16.4, p<0.001) and only the scanner-digitised images were used in further analysis.

Figure X-1: Relative warp scores for all digitised images. Each point is the same but uses different symbols to differentiate categories. Centroid size is indicated by the diameters of the circles. In each graph, the box shows the legend of the symbols of the figures. Digit: digitizing method; Photo: images aquired with a cammera; Scan: images aquired with a flat scaner; Sector: geographic location of the speciemens; ALIC: Alicante; DELT: Ebro delta; EALB: East Alborán; NCAT: North Catalonia; WALB: West Alborán Sea.
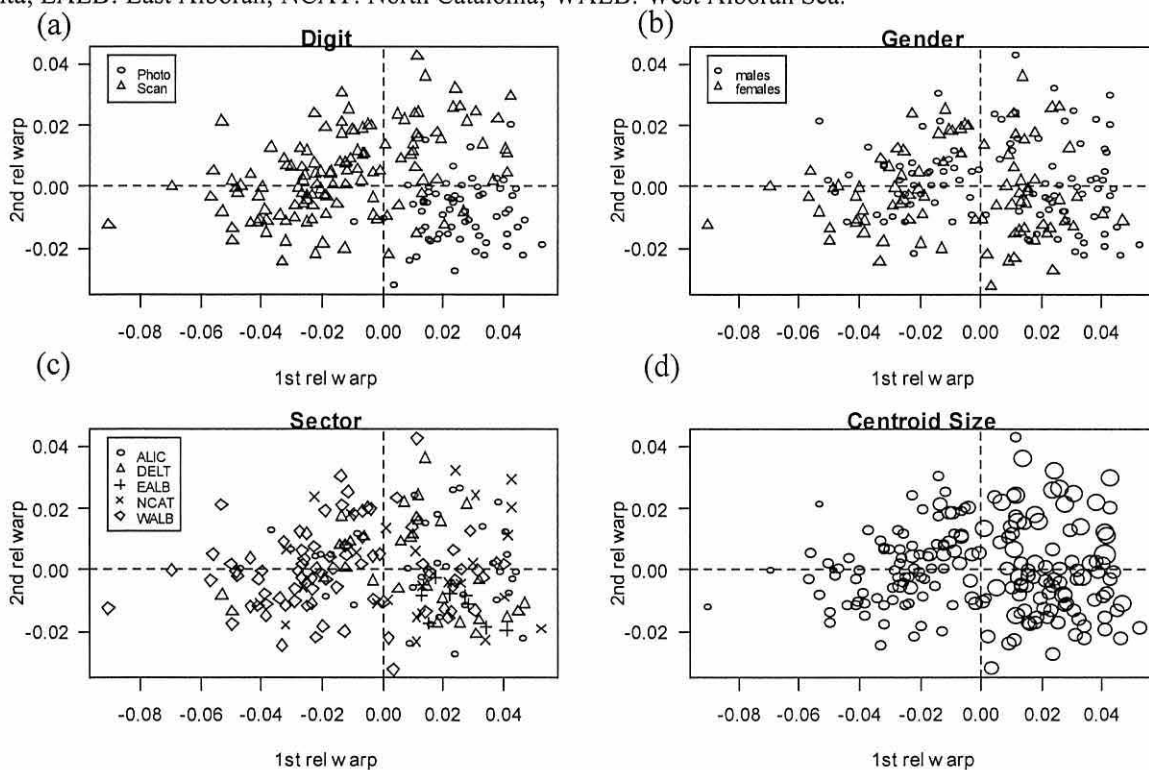
Figure X-1 b shows that male and female shape does not separate on either axis, although there was a general tendency for males spread further along axis one. The average centroid size for males ($\male$CS: 0.695 ± 0.02 $\log_{10}$(cm) ± SE) was significantly greater

($T_{[121]}$=2.05, p = 0.043) than that for females ($\female$CS: 0.640 ± 0.018 $\log_{10}$(cm) ± SE). Ordinations for location also show no great separation on either axis other than those from West Alborán, that showed a much reduced spread on axis one (generally smaller) and those from East Alborán all being large (positive on axis one).

Figure X-2 highlights the major shape differences (landmark positions) identified between the genders and southernmost to northernmost sampling locations. Any difference between males and females appears minor in comparison with that between northerly and southerly populations. Hence, there appeared to be more landmark differences between populations than between genders, although both involve changes in relative position of landmarks 15, 2, 3 and 12, which can be summarised by carapace width and length and width of the abdomen.

Figure X-2: Resistant Procrustes superimposition of the shape differences between males (continuous line) and females (dashed line), and between southern (continuous line) and northern (dashed line) locations, in each landmark (numbers). (see Figure IX-1 for the position of the landmarks). Note that the values were multiplied by three to improve visualisation.
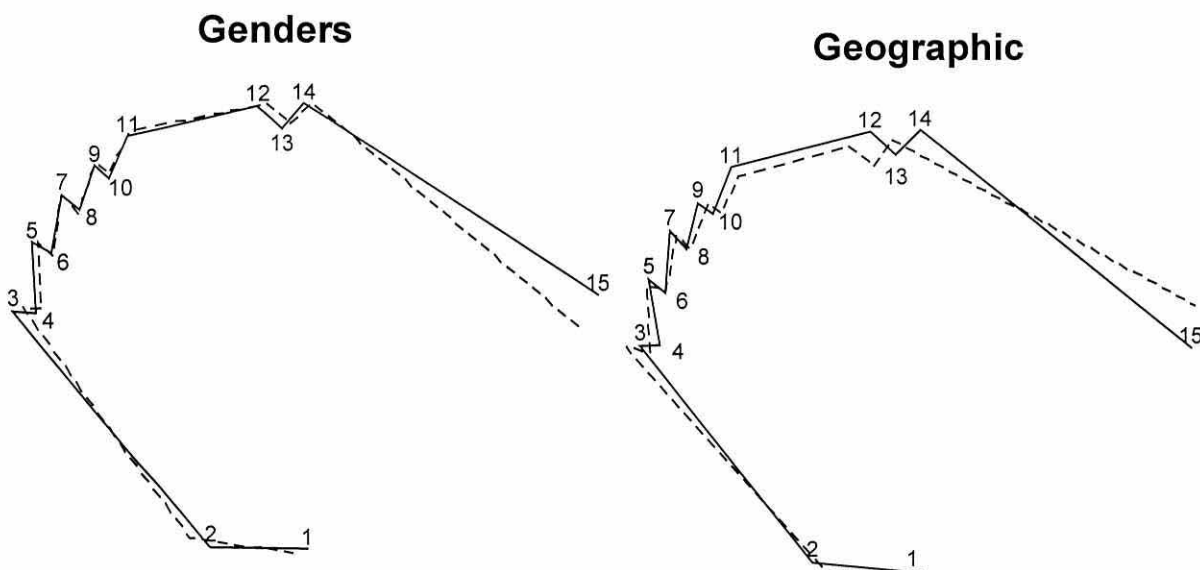
Table X-1a shows the results of the MANCOVA applied to the shape variables (partial warps and uniform components). The significant three-way interaction indicates that any differences in shape between sample locations, depends on which gender is considered and no uniform pattern in shape difference is detectable. Sampling location explained 12%, gender 4% and centroid size 35% of the variability in shape, leaving 49% unexplained. Similar results were obtained when the uniform components of shape variation were excluded from the analysis. The three-way interaction is not significant if the analysis is performed using crab images from Catalonia and Alicante only. There were then no significant differences between

male and female shapes but significant differences between shapes for crabs from Catalonia and Alicante (Table X-1b). Furthermore, significant interaction between location and $\log_{10}$ centroid size indicated a difference in the rate of shape change with growth between the two areas (Table X-1b).

Table X-1: MANCOVA results showing Pillai's statistic, applied to the partial warps and uniform component of carapace shape in *Liocarcinus depurator*. Log centroid size was used as a covariate. (a) all data (four geographic sectors: NCAT, DELT, ALIC and WALB); (b) only northern localities: north Catalonia, Delta and Alicante.

(a)	Statistic	F	DF		p
$\log_{10}$(CS)	0.898	28.491	26	84	<0.001
Gender	0.307	1.433	26	84	0.111
Sector	0.948	1.527	78	258	0.008
Gender × $\log_{10}$(CS)	0.330	1.594	26	84	0.058
Sector × $\log_{10}$(CS)	0.919	1.462	78	258	0.015
Gender × Sector	0.837	1.279	78	258	0.080
Gender × Sector × $\log_{10}$(CS)	0.890	1.396	78	258	0.028
(b)					
$\log_{10}$(CS)	0.956	17.893	26	21	<0.001
Gender	0.500	0.805	26	21	0.703
Sector	1.464	2.313	52	44	0.003
Gender × $\log_{10}$(CS)	0.497	0.798	26	21	0.711
Sector × $\log_{10}$(CS)	1.371	1.845	52	44	0.02
Gender × Sector	1.266	1.459	52	44	0.100
Gender × Sector × $\log_{10}$(CS)	1.288	1.531	52	44	0.075

Further analysis was carried out by using the dimensions indicated as showing the greatest variation in relative landmark position, and considering Delta and north Catalonia as one sector (CAT), to simplify the analysis (see Figure X-2). On average, measured crabs from the Alborán Sea tended to be smaller than crabs sampled further north (mean abdomen width: West Alborán = 0.79±0.04 cm, Alicante = 1.33±0.25 cm and Catalonia = 1.15±0.13 cm), because in the southern locations only small crabs were measured. Furthermore, the relationships between carapace width/length was allometric (Power function exponent = 1.047 ± 0.008 and 1.046 ± 0.007 for males and females, respectively). The ratio of carapace width/length, was similar in all three areas (mean width/length: West Alborán = 1.27, Alicante = 1.29 and Catalonia = 1.28). The relationships between $\log_{10}$ abdomen width and $\log_{10}$ carapace width across gender and location produced significant three-way interaction (3-way interaction: $F_{[1,49]}$=4.03, p=0.02) which is clearly shown by the parallel slopes for males and females from the northern crabs in relation to the different slopes for males and females in the south (Figure X-3). The relationships for the southern and northern crabs were thus re-analysed separately. Table X-2 shows that no interaction term was significant for the two northerly locations hence all slopes were parallel (3-way interaction: $F_{[1]}$=0.84, p=0.364).

However, there was a significant difference in intercept between males and females ($F_{[1,49]} = 4.03$, $p = 0.05$) thus over the size range examined females had wider abdomens. There were no significant differences in intercept between the relationships for crabs from either location ($F_{[1,49]} = 0.5$, $p = 0.481$).

In contrast, however, no significant differences between the slopes ($F_{[1,63]} = 0.91$, $p = 0.172$) or the intercepts ($F_{[1,63]} = <0.001$, $p = 0.955$) of the relationship abdomen width vs. carapace width, were identifiable within the size range measured for the crabs from West Alborán. However, examination of Figure X-3 shows that most female crabs over 1.6 cm in carapace width ($Log_{10} = 0.2$) appear above their male counterparts in a very similar fashion to those crabs from the northern areas over the whole size range measured. Females less than 1.6 cm in carapace width (and several up to 2 cm, $Log_{10} = {\sim}0.3$) are intermingled with their male counterparts.

Figure X-4 shows the relationships between *L. depurator* Log_{10} abdomen width and the Log_{10} ratio of carapace width to carapace length for each sample location. The crabs from the Alborán Sea had a much smaller increase in abdomen width as the width to length ratio increased than did those crabs collected from Alicante and North Catalonia. The width of the abdomen in short, wide crabs (generally older crabs) was considerably less for crabs from the southeast than that in equivalent sized crabs from the more northeasterly areas.

Figure X-3: Relationship between log_{10} abdomen width and log_{10} carapace width of males (+ and continuous line) and females (o and dashed-dotted line) *L. depurator*, in North Catalonia and Alicante (a) and west Alborán sea (b).

a) Northern locations (Catalonia and Alicante)   b) West Alborán (different scale)
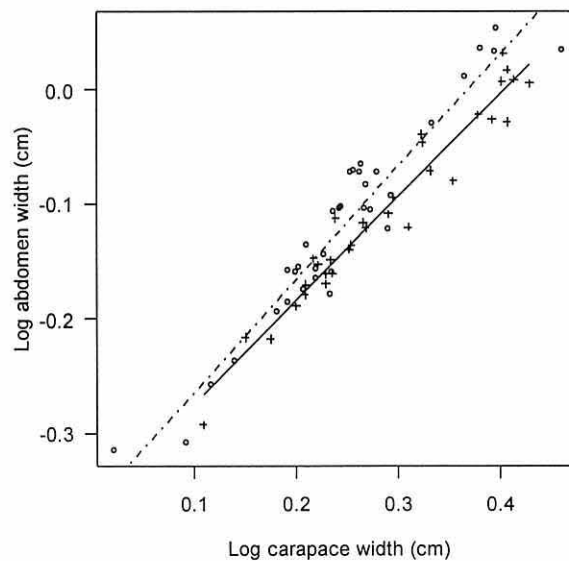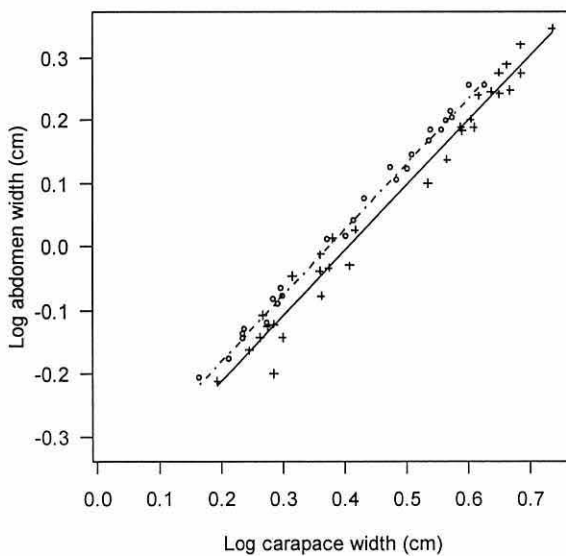
Table X-2: Results of an analysis of variance of Log_{10} carapace width and Log_{10} abdomen width of *L. depurator* in northern Mediterranean coast of Spain (Alicante and Catalonia). Sums of squares are adjusted for entry order.

(a) Slopes and intercepts for northern crabs

| | Location | | | | Mean | |
| | Alicante | | Catalonia | | | |
	slope ±SE	Intercept ±SE	slope ±SE	Intercept ±SE	slope	Intercept
Males	1.066 ± 0.045	-0.436 ± 0.025	0.999 ± 0.039	-0.404 ± 0.019	1.033	-0.42
Females	1.027 ± 0.021	-0.381 ± 0.009	1.032 ± 0.023	-0.386 ± 0.1	1.03	-0.384
Mean	1.047	-0.409	1.016	-0.395	1.032	-0.402

(b) Analysis of variance table for northern crabs

Variable	DF	Sum Squares	Mean Adj SS	F	p
Gender	1	0.00962	0.00190	4.03	0.050
Sector	1	0.03373	0.00024	0.50	0.481
Log_{10}Width	1	1.42916	1.32700	2822.39	<0.001
Gender × sector	1	0.00003	0.00049	1.04	0.313
Gender × Log_{10}Width	1	<0.00001	<0.00001	0.01	0.940
Sector × Log_{10}Width	1	0.00049	0.00030	0.63	0.432
Gender × sector × Log_{10}Width	1	0.00039	0.00039	0.84	0.364
Error	49	0.02304	0.00047		

(c) Slopes and intercepts of Alborán crabs

Gender	Slope ±SE	Intercept ±SE
Males	0.988 ± 0.050	-0.362 ± 0.013
Females	0.899 ± 0.039	-0.363 ± 0.012
Mean	0.944	-0.363

(d) Analysis of variance table for the Alborán crabs

Variable	DF	Sum Squares	Mean Adj SS	F	p
Gender	1	0.00228	<0.00001	<0.01	0.955
Log_{10}Width	1	0.43993	0.43581	862.20	<0.001
Gender × Log_{10}Width	1	0.00096	0.00096	1.91	0.172
Error	63	0.03184	0.00051		

Figure X-4: Exponential relationship between abdomen width and carapace width/length in male and female *Liocarcinus depurator* sampled from the West Alborán Sea (ALBO)(● and dashed line), Alicante (ALIC)(○ and dashed-dotted line) and North Catalonia (NCAT)(+ and continuous line). The relationships are fitted by least squares regression.
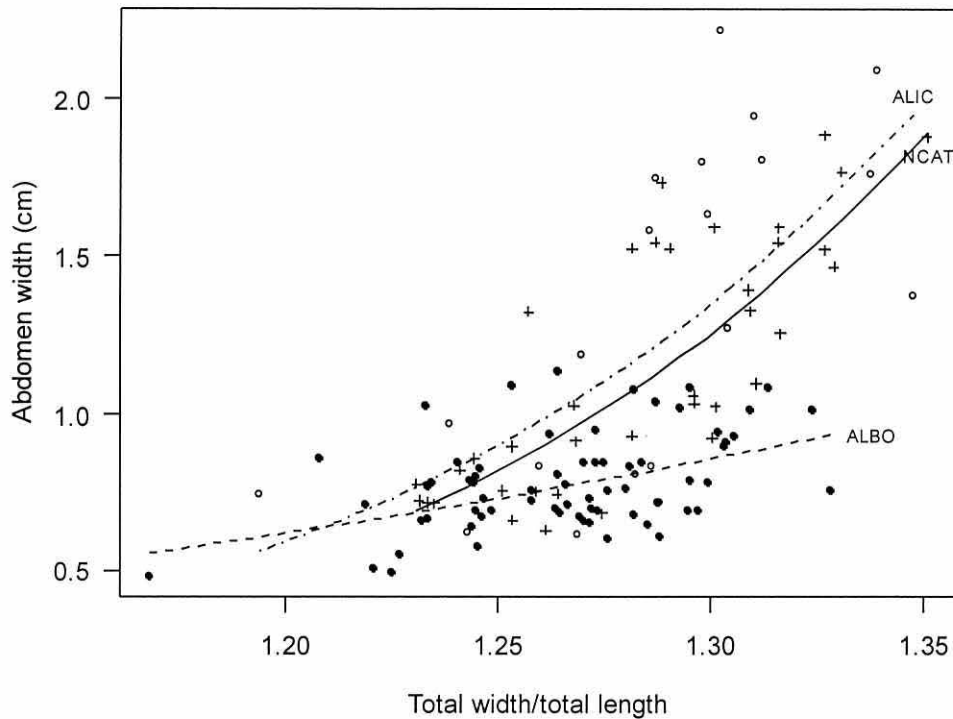
Table X-3: Results of an analysis of variance using Log_{10} ratio of carapace width to length as a covariate, comparing the relationships between log10 abdomen width and Log10 ratio for male and female *L. depurator* from 3 areas of the Mediterranean coast of Spain. Sums of squares are adjusted for entry order.

(a) Slopes ± SE

Location	Males	Females	Average
West Alborán	3.5 ± 1.7	1.8 ± 1.2	4.4 ± 1.2
Alicante	10.4 ± 2.3	9.8 ± 2.2	10.1 ± 1.5
North Catalonia	11.3 + 1.7	7.4 ± 1.8	9.4 ± 1.3

(b) Analysis of variance table

Variable	DF	Sum Squares	Adj Mean SS	F	P
Gender	1	0.02356	0.01185	1.35	0.248
Sector	2	0.91768	0.04380	4.98	0.009
Log_{10}Width/Length	1	0.62676	0.71315	81.16	<0.001
Gender × sector	2	0.00178	0.00269	0.31	0.737
Gender × Log_{10}Width/Length	1	0.03372	0.01094	1.24	0.267
Sector × Log_{10}Width/Length	2	0.13959	0.06667	7.59	0.001
Gender × sector × Log_{10}Width/Length	2	0.00742	0.00371	0.42	0.657
Error	105	0.92268	0.00879		

Table X-3 shows the results of a comparison of the regressions between Log_{10} abdomen width and Log_{10} ratio of carapace width to length in *L. depurator*. A highly significant overall regression is indicated ($F_{[1,105]}$ = 81.16, p <0.001) and the only significant interaction term showed differences in slope between sampling locations ($F_{[2,105]}$ = 7.59, p = 0.001). Table X-3 shows that the slopes for both Alicante crabs and those from North Catalonia were similar (no significant difference Bonferoni $CI_{95\%}$ on the difference = 0.7 ± 3.4) but both slopes were 3 – 4 times greater than that for crabs sampled in West Alborán (significant, Bonferoni $CI_{95\%}$ = 7.1 ± 3.04) Within the errors of measurement, there were no significant differences in slope between males and females irrespective of sample location ($F_{[1,105]}$ = 1.24, p = 0.267) although the slope for females was always less than that for males.

X-5. DISCUSSION

Aldrich (1993) suggests that crustacean taxonomy and even shape differences between local populations of the same species can be reliably examined by using a global approach to shape analysis through geometric morphometry. The present study shows that the application of geometric morphometric analysis to *Liocarcinus depurator* carapace shape provides results that are interpretable in terms of the organisms biology even though the differences may be small. The inability of multivariate statistics to separate the populations probabilistically results from significance in a high order interaction term which is notoriously unstable under MANOVA (see Table X-1). The interaction undoubtedly arises because of the relative growth differences between males and females from the southerly populations and those in the north (see Figure X-3).

It is clear from the current study that the digitising method greatly influences the results of the morphometric analysis. The digital camera produced images that probably resulted in more variability for a given crab's size and had a distinct systematic departure from those obtained from the scanner. With potentially greater resolution and a fixed relationship between specimen and transducer, the scanner provided a much more realistic spread in size and shape of the *L. depurator* carapaces. As in all scientific endeavours it is essential to find the appropriate tool with the correct resolution to tackle the problem. Furthermore, it is abundantly clear that images captured by one device are unlikely to match those captured with another, hence mixing tools in a single investigation will undoubtedly compromise the result. A previous study has already highlighted the problem (Corti M. pers. com.) where image capture of the same specimens by two different digital cameras gave quite contrasting results when ana-

lysed. The prooving of novel or little documented techniques should be uppermost in any investigator's mind prior to data collection let alone analysis.

Unlike in the current study, Abelló (1990a) failed to detect sexual dimorphism in *L. depurator* carapace shape through non-geometric morphometry. The current study and Rufino *et al.* (2004), however, showed that female *L. depurator* have a wider abdomen base than the males using both geometric and non-geometric morphometry. A wider abdomen may result in a greater relative volume for gonad development but should certainly provide a relatively greater surface for egg carrying as in many other Brachyurans (see: Hartnoll, 1985; Hartnoll, 1982). The present results not only demonstrate that females have wider abdomens than males but that wider abdomens are associated with both males and females as the width to length ratio of the carapace increases. The relationship between carapace width and length is allometric with crabs tending to get wider rather than longer as they grow. Of course, the current study infers abdomen width from landmarks 1 and 2 (see Figure X-2) on the carapace and none of the actual abdominal segments were measured. Differences in the abdominal width of most brachyurans show sexual dimorphism to occur over the last few segments rather than the first.

The geometric morphometry helped identify areas of the carapace showing greatest variability across sample locations hence prompted the choice of linear dimension analysis used to examine the underlying differences identified through the multivariate analysis of the shape variables.

The relationship between the width of the abdomen and the ratio of carapace length/width differed significantly with a much lower rate of abdomen increase with ratio in the southern samples in comparison to those from further north. Although crabs measured from the Alborán Sea were smaller than those of the northern areas, there was still a considerable overlap in size range of crabs between the three samples. The width/length ratio increases as the crabs get bigger (older) hence the broadening of the abdomen is much less pronounced with age in crabs from west Alborán. Indeed, it would appear that southern crabs with smaller width/length ratios actually have wider abdomens on average than their counterparts in the north.

The Mediterranean coast of Spain, close to Gibraltar is heavily influenced by the influx of relatively cold nutrient rich Atlantic water. This cold water mixes with warmer water of largely Mediterranean origin in the Alborán Sea. The waters off Alicante and Catalonia originate from the mixing of a southerly Atlantic current flowing along the coast of Algeria and water from the Ligurian Sea in the west. Thus, the Atlantic influence is much less pronounced on the Northern Spanish coast than it is in the South. Given the high influx rate of Atlantic

water it is feasible for larvae from populations outside the Mediterranean to gain access and potentially establish themselves in the Alborán Sea. It seems much less likely that such incoming larvae could undertake such a large journey, with the Algerian current and mix with populations in Catalonia or Alicante. Maldonado (1995, fish) and Abelló (2002, decapods) have both shown that community structure in the Alborán sea can exhibit characteristics more closely resembling Atlantic assemblages of the same species than those found in the rest of the Mediteranean. De Grave & Diaz (2001) compared the morphology (linear dimension analysis) of Mediterranean and Atlantic populations of the crangonid *Pontophilus norvegicus*. They found that telson length, antennal scale width and the presence of a tubercle on the dorsal carina and carapace showed discriminating power for separating populations from the Atlantic and the Mediterranean. In general, morphological variability between populations is attributed to genetics and/or different environmental conditions.

The environmental conditions of the Alborán Sea are roughly similar to those on the northern Mediterranean coast of Spain hence it is possible that the Alborán sea population of *L. depurator* is largely recruited from the Atlantic rather than the Mediterranean. In Atlantic waters, marine species tend to reach larger sizes. It is possible that the slower increase in abdomen width with carapace width/length ratio indicates a later onset of maturity in the Alborán sea. Figure X-3a shows no evidence of a major maturity shape change for crabs in the North yet clear evidence of shape change at a given size range for crabs from the Alborán sea (Figure X-3b). Given the average temperatures in the Atlantic are lower than in the Mediterranean, the growth rates in the Atlantic are likely to be lower then those for the Mediterranean coast. Accordingly, the likely slower growth rates in Atlantic species are possibly accompained by a retarded rate of maturity which is reflected in the Alborán crabs but not in the crabs from the Catalan and Alicante coasts. The paucity of small specimens (< 1.6 cm carapace width) from the northern samples and large specimens from the Alborán area (Figure X-3a) negates further conclusion from the current data.

XI. Discussion

It is now clearly appreciated that proper management of an otherwise declining fishery or any exploited ecosystem requires a fundamental understanding of all aspects of that system. Approaches that have focused only on the exploited species have failed repeatedly. Thus, the consideration of other species within exploited communities is an essential requisite to managing any marine system. Mediterranean fisheries are characteristically multi-specific and many of the captured species are consumed. The volume of by-catch is, however, still large. This thesis is focused on ecological aspects of the portunid crab, *Liocarcinus depurator,* which represents the main crustacean by-catch in commercial trawls shallower than 200 m along the Mediterranean coast of Spain. The importance of *L. depurator* has been widely recognised, not only numerically, but both as a predator and a prey in the ecosystem interaction web (section I).

The distribution of the organisms can be analysed through several techniques, which require different levels of mathematical and statistical comprehension. The different methods provide different sorts of information about the species.

Measurements of *L. depurator* densities were obtained from a ten-year time series of bottom, otter trawl surveys, covering a depth range of 25-800 m along the Mediterranean coast of Spain (from Gibraltar to Rosas, see section II). The simplest approach employed divided the Spanish coast into eight geographic sectors and the depths into discrete intervals (section III). Inference was then based on difference between medians or means in the light of their associated variability. This approach gave information on the overall patterns, although in most cases the high variability in the data coupled with the relative low number of samples in some factor levels hindered interpretation. On average then, *L. depurator* distribution and abundance appeared to be delineated by depth (see Figure III-2) such that highest abundance occurred in the shallower samples (51-150 m). Density was fairly constant down to about 301-400 m although crab occurrence exhibited a second potential mode at around 301-400 m. *L. depurator* was increasingly scarce below 500 m and virtually absent below 700 m. A similar distribution has been noted in the Western Mediterranean (Abelló *et al.*, 2002), but never observed in such detail over an area as large as the current study. Since depth is such a limiting factor for *L. depurator*, the distribution of the crab with depth was relatively clear despite the wide variation in density measurements obtained, by combining the results from a wide geographic area over 10 years.

Annual variability in *L. depurator* density presented a less straightforward interpretation since at least two trends were present and the variation with depth appeared to differ between years with little apparent pattern, thus increasing variances. Over the ten-year period a general downward significant trend both in crabs occurrence and density, were apparent. Potentially superimposed, however, was a cyclical trend in abundance with an approximate periodicity of 3-4 years. Cycles of low and high population abundance have been shown for several species but not previously for *L. depurator* in the Western Mediterranean. If *L. depurator* has a life span of 3-4 years, the potential periodicity of the population abundance would fit perfectly with our data. However, there is no available study on this specie's logetivity. Thus the cycle may be driven by the occasional high recruitment in certain years followed by a steady decline in population numbers as that year class dies out. Occurrence (potentially habitat occupancy) of *L. depurator* follows a very similar potential cycle indicating greater habitat occupancy when densities are highest.

Liocarcinus depurator densities tended to be highest where the continental shelf was wider. Areas like East Alborán and the Gulf of Vera which have particularly steep shelf slopes, and presumably very little muddy substrata, had the lowest crab densities. However, with such strong effects of year and depth compounded in the average (or median) estimates of density for geographic locations resulted in very high confidence intervals and any detailed differences between areas were not significant. The delineation of the areas for comparisons within the study was at best convenient and at worst arbitrary. Any conclusions drawn from differences between crabs in particular areas must clearly depend on the characterisation of the areas. There are various generalisations that characterise certain of the areas (wide continental shelf, steep shelf slope, muddy substrata etc.) and they have been chosen specifically by those characteristics. However, the size of the areas and their latitudinal or longitudinal extent reflects mostly, a convenient apportionment of coastline. It is little wonder, then, when attempts to consider crab density distribution differences in relation to depth and year between areas founders in a sea of variability. The simple approach is thus fraught with difficulty because of the inability to define the variability precisely (arbitrary geographic areas) or the variable of interest becomes discrete rather than continuous (depth intervals as opposed to actual depth) which inevitably leads to a loss of variability when group means are examined. Furthermore, the inevitable interaction effects derived make it impossible to interpret the effect of each factor separately.

A more sophisticated approach is to attempt modelling, on a continuous scale, to estimate variability associated with measured influences and attempt to ascribe probability levels to the effects or differences (section III). In this approach, depth was considered as a continu-

ous variable, which is certainly more realistic than dividing it into intervals. However, the study area stretched from north east to south west, making latitude and longitude an unhelpful continuous variable to model, hence geography still had to be interpreted through discrete areas. The densities of *L. depurator* were thus subjected to analysis through linear modelling but with limited success, highlighted by the low percentage of explained variance (see Figure III-13 a-c). The generalities of distribution with depth were reasonably well approximated by linear and quadratic terms in depth but only when the depth distribution was split in two, either side of 150 m depth. Maximum *L. depurator* densities were estimated to be located around 80 m, similar to that found off Málaga (García-Raso, 1984, maximum densities between 36 and 90 m), in the Ligurian Sea (Mori & Zunino, 1987, maximum densities at 90 m), in the Catalan Sea (Abelló, 1986; Abelló *et al.*, 2002, maximum densities between 50 and 100 m) and off Cyprus (Demetropoulos & Neocleous, 1969 in: Lewinsohn & Holthuis, 1986, from 73 to 110 m)

Density of *L. depurator* decreased significantly from 1994 to 2003 but at a greater rate of decline (8% pa.) in shallower water (<150 m), where crab densities were greater. The modelling approach had the advantage of ascribing statistical significance to the trends and partitions the effect of each variable on the total variance, both separately and in combination. The basic assumptions of parametric analysis, however, are often difficult to meet with biological data. Methods such as generalised additive models, may overcome such assumptions and linearity but inference and the interpretation of the results can become difficult (Quinn & Keough, 2002). To the author's knowledge, no previous study has attempted to model temporal changes of *L. depurator* densities through linear models.

Another approach is based on geostatistical modelling, where the correlation between neighbouring samples ('spatial autocorrelation') is modelled and the model used to produce potentially continuous density estimates from the sample data over the entire sampled area (section IV). Because the data were highly skewed and the sampling density low relative to the sampled area a preliminary study of how changes in geostatistical methods affected the final estimates was crucial to interpreting the outcome in relation to the limits of the analysis (section V). Unremarkably, the largest influence on the outcome revolved around choice of attempted data normalisation. Taking logs of the densities produced totally unrealistic results while omitting up to 8% of the densities as outliers provided relatively stable estimates. Secondly, the choice of spatial resolution as determined by the number of distance classes over which to average the variances was a crucial step in deriving stable estimates. Other than the choice of model to fit to the experimental semi-variograms, most of the other 'geostatistical options' made virtually no difference to the general interpretation. Remarkably, the choice of

model to fit made on a moderate impact on the estimations since in most instances the models were fitted to less than five functional points. The most appropriate (as defined by stable and realistic density estimates) methodological options were then used to estimate *L. depurator* densities from 1994 to 2003 (section VI). Depth was incorporated in the model as a covariate, both in the calculation of the variogram and in the interpolation of the density estimates. Thus density was modelled as a function of depth and geography, both treated as continuous variables. The density maps produced (see Figure VI-3) permitted a detailed examination of variation throughout the sampled area and the exact location of the high-density areas that could then be interpreted in the light of oceanographic phenomena. When overall densities were lower, higher *L. depurator* density coincided with areas of high primary productivity that were either related to coastal up-welling (west Alborán) or river outflow (Ebro Delta). Hence, those two locations can be important for the conservation of this species. The geostatistical approach fails to provide an ready quantification of the tendencies from year to year and falls short of indicating statistical significance except in the broadest terms. Recent studies, however, attempt to derive both quantitative trend estimates and robust statistical inference from geostaticial analyses (Pebesma, 2002, for example).

In the small scale study, off the Ebro Delta, the distribution of *L. depurator*, as estimated from geostatistics, was significantly correlated with that of several sediment characteristics (sediment temperature, organic matter concentration and redox potential), although the overall level of spatial overlap was low (section VII). Furthermore, residual weights from the relationship between *L. depurator* density and biomass were analysed and mapped to identify any segregation of the crabs by size. Smaller individuals on average were found more often at shallower depths than larger crabs. The geostatistical approach can be criticised because the significance of the spatial correlations were based on interpolated values and not on measured values. Thus a considerable degree of 'faith' in the technique is required and the investigator must be satisfied that an adequate number of measured values have been obtained over a spatial scale that fits the environmental heterogeneity. The adequacy of sample cover has three major effects on the analysis: (a) insufficient numbers of samples are likely to lead to a poorly estimated spatial model, (b) few samples are unlikely to detect the degree of environmental heterogeneity needed for adequate correlation between distributions and (c) contouring between limited numbers of points shows no more than general trends and can be completely unrealistic if the interpolations were initially based on an inadequate spatial model. A major problem is the difficulty involved in identifying how realistic the interpolations are when sample measurements are low in number. These approaches have been often attempted using GIS, where several maps can be overlaid and spatial overlap quantified, thus providing a sce-

nario where all variables are treated continuously through space. Even then, the expectation is that the maps are a good, not just adequate, representation of the distributions.

Differences in the sampling protocol (trawl mesh size and duration, etc.) between the large scale (Mediterranean coast of Spain) and small-scale (off Ebro Delta) study did not permit any further detailed comparison between *L. depurator* density. The resource allocation in any scientific survey are should be so that the maximum amount of information can be extracted from the survey. Frequently such is not the case and ancillary data sets (e.g. the Ebro Delta *Liocarcinus* densities) are often compromised through allocation of insufficient resources. The additional information acquired is thus often difficult to analyse and interpret showing larger variability than would have been desirable. Since much of the data presented in the current thesis come as a by-product of a larger venture it suffers from less than adequate resourcing. The author recognises that the application of geostatistics to the *L.depurator* distribution pushes the limits of the technique in anticipation of providing useful ecological information in a constructive way from an otherwise limited set of measurements.

The analysis of *L. depurator* distribution (section III and VI) coupled with information on the western Mediterranean circulation (section II) suggested the hypothesis that crab populations from the Alborán Sea were different from those in the northern part of the study area. Differences between Atlantic and Mediterranean crustacean populations have been reported in detail for *Pontophilus norvegicus* (De Grave & Diaz, 2001) and in general for many other species (d'Udekem d'Acoz, 1999). However, the differences were taxonomic i.e. the presence of spines or tubercles, without no inferred ecological basis. The major differences in salinity, temperature, nutrient content and presumably origins of any larvae carried between the Atlantic and Mediterranean waters may encourage distinct populations in different parts of the Mediteranean. If the populations have ecological and/or genotypic divergence it will most likely be reflected in the organism's shape. Crustaceans in particular, with their hard exoskeletons are very likely to exhibit shape differences between populations.. The density maps (Figure VI-3) clearly shown the existence of two centres of maximum abundances, one in the Ebro Delta, which could be representative of Mediterranean populations and the other in Western Alborán which is much closer to Atlantic populations of *L.depurator*. To determine possible differences in shape between geographic locations within the western Mediterranean, a combination of traditional morphometry and the more recently developed geometric morphometry were utilised.

The novelty of geometric morphometry methods required another brief introduction in the thesis (section VIII) and again some basic procedures within the analysis were tested. Thus, the effect of specimen preservation by alcohol or freezing (section IX) and the method

of digitising images of the specimens (flat bed scanner or digital camera) were examined (section X). Only global differences in shape were caused by preservation method, i.e. all specimens shrank with no differential shrinkage between different parts of the carapace. However, the digitising method produced a systematic error between the variables defining carapace shape that was much greater than any differences between specimens. The importance of always using the same digitising tool and procedures was thus highlighted. The carapace shape of *L. depurator* was studied in relation to the size of the organism, gender and geography (section X). Landmarks showing greatest variability were identified, and the corresponding linear dimensions (carapace width and length and abdomen width) were taken as gender and geography could not be separated in the shape analysis due to a significant interaction in the multivariate analysis. Crabs from the Alborán Sea were clearly differentiated from those of the northern locations in the relationship of abdomen width and the ratio between carapace width/length. Although only small specimens were represented in the Alborán samples, the overlap in sizes and clarity of the differences permitted the comparison.

The presence of a hard exoskeleton turns crustaceans into an excellent group for the applications of geometric morphometry, as the exoskeleton remains rigid after death and positional interrelationships between homologous parts of the skeleton do not distort if specimens are properly preserved. The use of the carapace spines as landmark points, in the current study, should be interpreted as a compromise between accuracy of location and potential homology. The spines can be easily damaged hence may reduce sample sizes significantly by having to exclude crabs with broken spines from any analysis. Furthermore, no histological or embryonic development studies have established carapace spines as homologous between species. The development of methods based on fewer landmarks, but with increased power to detect small shape changes will surely improve shape analysis in crustaceans (e.g. sliding landmarks, analysis of curves). Alternatives, such as contour analyses, could not detect shape changes (unpublished data), probably due to low sensitiveness of Fourier analysis applied to this technique. According to Rohlf & Corti (2000), the fundamental advances of geometric morphometry over traditional approaches are in the development of powerful statistical methods designed for analysis of shape rather the use of multivariate methods on *ad hoc* collections of distances, angles and ratios.

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XII. References

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Index

128, 129, 130, 131, 133, 134, 136, 140, 143, 144, 146, 148, 149, 152, 153, 163, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 176, 177, 178, 179, 180, 183, 185

Solenocera membranacea, 86, 88, 89

Spain, 1, 16, 18, 19, 22, 25, 26, 27, 28, 29, 30, 31, 35, 36, 39, 40, 47, 57, 58, 59, 61, 62, 65, 66, 67, 69, 86, 87, 88, 89, 90, 92, 95, 107, 114, 115, 127, 132, 174, 175, 181, 182, 184, 185

Spanish, 1, 39, 40, 48, 52, 55, 58, 63, 85, 93, 101, 114, 115, 116, 119, 122, 184

spatial dependence, 79, 103, 104, 105, 127, 135

spatial structure, 1, 21, 31, 75, 76, 81, 86, 93, 100, 105, 112, 113,

114, 115, 116, 117, 118, 127, 129, 131, 132, 138, 142, 143

Species, 75, 86, 87, 88, 89, 115, 162

Sprattus sprattus, 167

Strait of Messina, 22

T

Tiber estuary (Italy), 16, 22

trawl, 1, 15, 16, 20, 23, 24, 25, 26, 27, 28, 29, 30, 36, 37, 38, 39, 40, 56, 57, 74, 85, 86, 92, 94, 95, 113, 114, 115, 116, 117, 128, 132, 133, 134

trend, 61, 62, 63, 64, 68, 69, 74, 76, 83, 95, 97, 100, 111, 112, 117, 118, 124, 127, 129, 130, 132, 135, 136, 137, 138, 139, 140, 143

U

Uca, 166

Uca pugnax, 33, 163, 166, 175

uniform shape, 172

universal kriging, 76, 95, 97, 99, 130

up-welling, 48, 52

V

variogram, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 86, 90, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 107, 111, 112, 113, 114, 116, 117, 118, 121, 122, 128, 130, 135, 136, 138, 139, 140, 142, 143

W

Walney Island (Wales), 26, 28